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Rundschreiben betreffend Dr. Ernst PRIESNER

Sehr geehrte Damen und Herren,
liebe Kolleginnen und Kollegen

falls Sie es nicht schon von Freunden erfahren haben, möchten wir Ihnen mitteilen, daß unser Kollege Dr. Ernst Priesner seit Mitte Juli 1994 verschollen ist. Als Ergebnis intensiver Suchaktionen durch Freunde, Bergrettung, Hundestaffeln, Hubschrauber und Polizei, die leider erfolglos verliefen, muß davon ausgegangen werden, daß er durch einen Unfall im Gebiet des Pflegersees bei Garmisch in den Bayerischen Alpen ums Leben gekommen ist.

Wie Sie alle wissen, hat sich Ernst Priesner seit vielen Jahren intensiv mit der Lockstoffsystematik beschäftigt und in dieser Fachdisziplin eine Weltspitzenstellung eingenommen. Zahlreiche Fachkollegen hatten mit ihm Kontakt und unzählige gemeinsame Projekte wurden durchgeführt bzw. sind noch im Gange. Das mutmaßliche Ableben von Ernst Priesner ist nicht nur für die Wissenschaft ein unersetzlicher Verlust, es werden sich dadurch auch für viele Kollegen große Schwierigkeiten bei ihren weiteren Arbeiten ergeben.

Deshalb gilt es sofort, den umfangreichen und für die Wissenschaft unersetzlichen Nachlaß zu sichern, ihn sicher und übersichtlich zu lagern und für die Zukunft verfügbar zu halten. Ferner müssen alle Bemühungen dahin gehen, möglichst wenig Information aus nicht abgeschlossenen, laufenden Projekten zu verlieren und wichtige Daten jenen Kollegen zukommen zu lassen, deren Arbeiten beeinträchtigt werden oder ein Ende finden müssen.

Das Max-Planck-Institut in Seewiesen sieht sich außerstande, die umfangreiche Bücher, Sonderdrucke, Karteien, handschriftlichen Notizen, Sammlungsteile, Negative, Fotos und Dias sowie die noch in den Labors vorhandenen Duftstoffe und ihre Komponenten zu lagern und evident zu halten. Vielmehr wird dort dringend Labor- und Büroplatz benötigt.

Nach Absprachen zwischen Frau Hedi Priesner, Prof.Dr. Kaissling, dem Arbeitsgruppenleiter von Dr. Ernst Priesner am Max-Planck-Institut in Seewiesen, Dr. Gerhard Tarmann vom Tiroler Landesmuseum in Innsbruck und nach Genehmigung des Direktors des Institutes, Herrn Prof.Dr. Eberhard Gwinner, ging der gesamte Bestand, mit Ausnahme des chemischen Teils (Pheromone und die Substanzen zur Herstellung), geschlossen an das Tiroler Landesmuseum Ferdinandeum (Naturwissenschaften), da dort im neuerbauten Institut ausreichend Raum für eine Lagerung und Betreuung vorhanden ist. Die Bearbeitung der Bestände soll durch folgende Maßnahmen gesichert werden :

1. das Max-Planck-Institut leistet einen finanziellen Beitrag ;

2. das Tiroler Landesmuseum Ferdinandeum setzt seine Mitarbeiter zur Betreuung der umfangreichen Literatur (hunderte Bücher, tausende Sonderdrucke und Kopien), der Sammlungen und des Fotoarchives ein und wird sich bemühen, weitere Mitarbeiter für die Katalogisierung (EDV-mäßige Aufarbeitung) zu bekommen ;

3. aus dem Verkauf von Literaturdoubletten (Bücher und Zeitschriften, die am Ferdinandeum bereits vorhanden sind) sollen weitere Mittel zur Betreuung des Nachlasses, vorallem zur Katalogisierung und Evidenthaltung der zahllosen handschriftlichen Notizen und der Originalprotokolle aus den Gelände- und Laborarbeiten verfügbar gemacht werden ;

4. es wird ein Fond zur Bearbeitung des Nachlasses Ernst Priesner eingerichtet ; alle Kollegen, denen die rasche Aufarbeitung des wissenschaftlichen Nachlasses ein Anliegen ist, da sie Informationen daraus immer wieder brauchen bzw. jene, die durch die Verbindung mit Ernst Priesner wesentliche Impulse für ihre eigenen Forschungen erhalten haben, könne sich durch einen finanziellen Beitrag beteiligen ;

5. für die Aufarbeitung des Nachlasses sollen sachkundige Mitarbeiter stundenweise engagiert werden.

Der chemische Teil des Nachlasses muß in kompetente Hände gehen, das heißt, in eine Institution, die fachlich und personell in der Lage ist, mit den Substanzen zu hantieren und eventuell nach publizierten oder aufgefundenen Rezepturen Pheromone weiter zu produzieren. Diese Möglichkeiten sind am Ferdinandeum in Innsbruck nicht vorhanden. Durch Intervention von Dr. Nils Ryrholm aus Uppsala ist es gelungen, bei Dr. Peter Witzgall in Lund in Schweden eine solche Möglichkeit zu finden. So können die laufenden Projekte vielleicht doch noch einen Abschluß finden. Auch Prof. Clas Naumann in Bonn wird sich bemühen, mit seinen Mitarbeitern Teilgruppen organisatorisch zu betreuen (besonders Sesien- und Zygaenenpheromone).

Wir möchten Sie bitten, falls sich für Sie wichtige Informationen in den vielen handschriftlichen Aufzeichnungen befinden, dies mit möglichst genauen Detailangaben mitzuteilen. Nur so gibt es eine Chance, gezielt zu suchen und Ihnen Informationen rasch zukommen zu lassen. Bitte wenden Sie sich an

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Wir hoffen, mit diesen Aktivitäten und Ihrer Hilfe wenigstens die große wissenschaftliche Lücke, die das mutmaßliche Ableben von Dr. Ernst Priesner für uns alle hinterläßt, so gering wie möglich zu halten.

Dr. Gerhard TARMANN

Summary

Dr. Ernst Priesner, the well-known pheromone specialist, has been missing since the middle of July 1994, when he went to check some pheromone traps in the Bavarian Alps, near Garmisch. Despite numerous search parties he could not be found and it must be assumed that he met with a fatal accident.

Dr. Priesner's contribution to pheromone research was immense and he led the world in the field of pheromone systematics. His research has resulted in an immense wealth of new faunistic and biological information. Many current scientific projects were dependent on his collaboration and their successful conclusion will now be very difficult.

It was therefore considered imperative to save and make available the vast and irreplaceable scientific material he left behind. Apart from the chemicals, the entire contents of Dr. Priesner's office and laboratory at the Max-Planck-Institute in Seewiesen, Bavaria, have been transferred to the Tiroler Landesmuseum Ferdinandeum in Innsbruck, Austria, under the charge of Dr. Gerhard Tarmann. This material consists of hundreds of books, thousands of scientific papers, card indexes, handwritten notes, photographs etc. A fund will be set up to finance the cataloguing and storage of the material. The Max-Planck-Institute will make a financial contribution and duplicate books will be sold. Donations to the fund are invited.

The responsibility for the chemical contents of Dr. Priesner's laboratory will be assumed by Dr. Peter Witzgall, Lund, Sweden, and Prof. Clas Naumann, Bonn, Germany will try to organise some of the projects (particularly those concerning sesiid and zygaenid pheromones). It is therefore hoped that the running projects can be brought to a conclusion.

If anyone requires specific information from Dr. Priesner's handwritten notes, he is invited to write to Dr. Gerhard Tarmann with as many details of the required information as possible.

It is hoped that the measures taken will ensure that the loss caused by Dr. Priesner's disappearance is kept to a minimum.

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Does ant-attendance influence development in 5 European Lycaenidae butterfly species? (Lepidoptera)

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Summary

Caterpillars and pupae of 3 myrmecophilous (*Aricia agestis*, *Polyommatus icarus*, *P. bellargus*) and 2 myrmecoxenous lycaenid butterflies (*Lycaena phlaeas*, *L. tityrus*) were reared in the laboratory together with, or without, 2 species of tending *Lasius* ants (*L. flavus*, *L. niger*). Duration of development, mass gain, growth rates, prepupal and adult weights, and the ratio of mass gain per frass production were studied. There was no evidence for significant developmental costs associated with myrmecophily. Rather, we found some marginally beneficial effects of ant-attendance. Males of *P. icarus* and *L. phlaeas* grew larger in the presence of ants. Mass gain per unit frass was slightly higher with ants in *A. agestis* (both sexes), *P. icarus* and *L. tityrus* (males only). We found no consistent differences between the effects of the 2 ant species, nor between rearing treatments involving 2 or 5 *L. flavus* workers, respectively. Sexual and interspecific differences were documented in most of the parameters. These results show that certain myrmecoxenous and facultatively myrmecophilous lycaenid butterflies are able to compensate for their energetic costs associated with myrmecophily. The evolutionary consequences of such low-cost mutualisms are discussed.

Zusammenfassung

Raupen und Puppen von 3 fakultativ myrmekophilen (*Aricia agestis*, *Polyommatus icarus* und *P. bellargus*) sowie 2 myrmekoxenen Bläulingsarten (*Lycaena phlaeas*, *L. tityrus*) wurden in Gegenwart von Ameisen (*Lasius flavus* bzw. *L. niger*) aufgezogen. Entwicklungsdauern, Wachstumsraten, Gewichte und Massenzunahme pro Kotproduktion wurden protokolliert. In keinem Fall ergab sich eine signifikante Beeinträchtigung dieser Parameter durch den Besuch von Ameisen und damit verbundene Sekretabgaben. Schwache positive

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Effekte konnten vereinzelt beobachtet werden (Gewicht der Männchen von *P. icarus* und *L. phlaeas* in Gegenwart von Ameisen größer, Massenzunahme pro Kotproduktion größer bei *A. agestis*, *P. icarus* und *L. tityrus*). Geschlechts- und Artunterschiede in den Entwicklungsparametern traten in den meisten Fällen auf. Die Ergebnisse zeigen, daß die untersuchten Bläulings-Ameisen-Interaktionen für die Schmetterlinge mit geringen, voll kompensierbaren Kosten verbunden sind. Die evolutive Bedeutung solcher Mutualismen mit niedriger Investition wird diskutiert.

Résumé

Chenilles et chrysalides de 3 Lycénides myrmécophiles (*Aricia agestis*, *Polyommatus icarus* et *P. bellargus*) et de 2 Lycénides myrmécoxènes (*Lycaena phlaeas* et *L. tityrus*) ont été élevées en laboratoire avec et sans 2 espèces de fourmis (*Lasius flavus* et *L. niger*). Les auteurs ont étudié la durée du développement, l'augmentation de taille, le taux de croissance, le poids des chenilles adultes et avant la chrysalidation, ainsi que l'augmentation de taille par rapport à la production d'excréments. Dans aucun cas, ils n'ont constaté une modification signicative de ces paramètres due à la visite des fourmis. Dans quelques cas, ils ont observé de faibles effets positifs de la myrmécophilie. Le poids des mâles de *P. icarus* et *L. phlaeas* augmenta en présence des fourmis ; l'augmentation de taille par rapport à la production d'excréments fut plus marquée en présence des fourmis chez *A. agestis* (dans les deux sexes), *P. icarus* et *L. tityrus* (mâles seulement). Les auteurs n'ont pas trouvé de différences consistantes entre les effets des deux espèces de fourmis, ni entre les élevages impliquant 2 ou 5 *L. flavus* (ouvrières). Des différences apparurent dans la plupart des paramètres du développement selon le sexe et l'espèce. Ces résultats montrent que les interactions Lycènes-Fourmis étudiées entraînent de faibles «coûts énergétiques», entièrement compensables. Les auteurs discutent de la signification évolutive de tels mutualismes «à faible coût».

Introduction

Many species of the butterfly family Lycaenidae live in association with ants throughout part of their larval and/or pupal stage (Cottrell, 1984 ; Pierce, 1987 ; Fiedler, 1991). Ant-associations among lycaenids range from loose and unspecific, facultative interactions to obligatory and species-specific cases of mutualism or, rarely, parasitism. Typically, while feeding on their hostplants, the caterpillars attract ants with the help of chemical stimuli. This ant guard may provide protection against parasitoids or predators (Pierce & Easteal, 1986 ; Pierce *et al.*, 1987 ; but see Peterson, 1993).

Interactions between lycaenid immatures and ants are mainly mediated by secretions from specialized exocrine epidermal glands (Malicky, 1969 ; COTTRELL, 1984), although vibratory communication may be important in certain cases (DEVRIES, 1990). Three types of myrmecophilous organs are known to play major roles. The dorsal nectar organ on the 7th abdominal segment, only present in larvae, secretes droplets of a clear liquid that contain carbohydrates and amino acids (MASCHWITZ *et al.*, 1975 ; PIERCE, 1983) upon tactile stimulation (TAUTZ & FIEDLER, 1992). So-called pore cupola organs, minute hair-derived glands distributed over the larval or pupal integument, appear to secrete amino acids or, in certain species, mimics of ant-pheromones (PIERCE, 1983). And the tentacle organs on the 8th abdominal segment of various lycaenid caterpillar species emit volatile compounds that cause an alerted behaviour in attendant ants (FIEDLER & MASCHWITZ, 1988 ; BALLMER & PRATT, 1992). All these secretions are produced at some energetic cost by the herbivorous caterpillars. In addition, the innervation and musculature of myrmecophilous organs and vibratory organs also cause metabolic costs.

Previous studies on two lycaenid-ant systems demonstrated that ant-attendance may have a negative impact on larval and pupal development. In the obligatorily myrmecophilous *Jalmenus evagoras* (DONOVAN, 1805) from Australia, ant-tended individuals develop faster than untended sisters, but attain lower weights (PIERCE *et al.*, 1987). Larvae of *J. evagoras* are unable to compensate for nutrient loss to ants (BAYLIS & PIERCE, 1992). As a consequence, myrmecophily is associated with significant fitness costs, since male mating success and female fecundity are strongly dependent on adult weight (ELGAR & PIERCE, 1988 ; HILL & PIERCE, 1989). In the Neotropical *Arawacus lincoides* (Draudt, [1919]), ROBBINS (1991) observed a slight retardation of larval development in response to ant-association, but weight was unaffected.

Recently, however, beneficial effects of ant-attendance on larval development have been detected in three additional species. FIEDLER & HÖLLDOBLER (1992) found that ant-tended males of the Palearctic *Polyommatus icarus* (Rottemburg, 1775) reach higher larval and pupal weights than untended controls. In the Nearctic *Hemiargus isola* (Reakirt, [1867]), tending by the ant *Formica perpilosa* enhanced caterpillar growth and thus adult weight, whereas two other ant species did not affect butterfly weight (WAGNER, 1993). These two butterfly species are facultative myrmecophiles, whose larvae associate with a variety of ant taxa and are not dependent on ant-association for survival. Overall, facultative myrmecophiles account for a larger proportion of the species diversity of the Lycaenidae than obligatory myrmecophiles (FIEDLER, 1991). Most recently, CUSHMAN *et al.* (1994) observed beneficial developmental effects in another Australian obligatory myrmecophile, *Paralucia aurifera* (Blanchard, 1848). Hence, the prominent developmental costs of myrmecophily as found in *J. evagoras* might be atypical for the species majority. Therefore, a better understanding of the evolutionary and ecological significance of developmental costs or benefits arising from myrmecophily among Lycaenidae butterflies requires experimental work on a larger set of species from various taxonomic groups and representing all major types of myrmecophily.

We here present the results of laboratory experiments with 5 European Lycaenidae species. Three of these possess all three types of myrmecophilous organs and are facultative myrmecophiles, but show different degrees of myrmecophily. While mature larvae of *Polyommatus bellargus* (Rottemburg, 1775) and *Aricia agestis* ([Denis & Schiffermüller], 1775) are rarely found without tending ants in nature, caterpillars of *Polyommatus icarus* are much less attractive to ants (e.g. Thomas & Lewington, 1991). *P. icarus* was included to repeat the experiments of Fiedler & Hölldobler (1992) under a modified rearing regime. We also studied two myrmecoxenous species : *Lycaena phlaeas* (Linnaeus, 1761) and *L. tityrus* (Poda, 1761). Larvae of these species neither possess a dorsal nectar organ nor tentacle organs, but they do have pore cupola organs. In laboratory experiments, weak and unstable ant-associations of these species can be induced and ants then harvest the PCO secretions (Fiedler, 1991). Neither *L. phlaeas* nor *L. tityrus* larvae have hitherto been observed in association with ants in the field.

Our aim was to investigate whether or not artificial ant-association involving two ant species and two different numbers of ants per individual lycaenid has any detectable effects on larval or pupal development. Furthermore, we wanted to know whether developmental effects differ between lycaenid species according to their degree of myrmecophily. One might expect more distinct costs in caterpillars that are highly attractive to ants (*P. bellargus*, *A. agestis*), whereas in myrmecoxenous species developmental costs should be absent or minimal. On the other extreme, secretion rates of obligatorily myrmecophilous caterpillars can be amazingly high (Fiedler & Maschwitz, 1989 ; Fiedler, unpublished), corresponding to the pronounced developmental costs observed in species like the Australian *Jalmenus evagoras* (Baylis & Pierce, 1992). Finally, the developmental constraints on phytopredacious lycaenid larvae parasitizing inside ant colonies (alike the Palaearctic *Maculinea* spp.) are entirely different (e.g. Thomas *et al.*, 1993, and references therein). Hence, a comparative survey across a larger number of species representing various stages of myrmecophily appears rewarding.

Material and methods

Butterfly rearing

Caterpillars were reared from eggs laid by field-caught (*Aricia agestis*, *Polyommatus bellargus*, *P. icarus*, *Lycaena phlaeas*, *L. tityrus*) or laboratory-bred females (*A. agestis*, *P. icarus*). Livestock originated from northern Bavarian populations except in *P. bellargus*, where part of the experiments was conducted with individuals from southern France. Butterflies were kept in a greenhouse for oviposition or mating. Rearing procedures largely followed those described by SCHURIAN (1989). Eggs were collected every second day and transferred into a climatic chamber (25° C, 16:8 h L:D), where the whole development to adult eclosion took place. Groups of first instar larvae were placed in translucent plastic containers (125 ml) lined with moist filter paper. They were fed with cut foliage or inflorescences of appropriate host-plants : *Geranium molle* L. (Geraniaceae) leaves (*A. agestis*) ; *Coronilla varia* L. (Fabaceae) leaves (*P. bellargus*) ; *Medicago sativa* L. (Fabaceae) inflorescences (*P. icarus*) ; *Rumex acetosa* L. (Polygonaceae) leaves (*Lycaena phlaeas*, *L. tityrus*). Food was exchanged daily. Special care was taken to provide food of approximately equal quality ad libitum throughout the season, since food quality may affect larval myrmecophily (FIEDLER, 1990 ; BAYLIS & PIERCE, 1991).

Ants

Two ant species were used. *Lasius niger* (Linnaeus, 1758) is a common species of open grasslands and is well known to tend a number of lycaenid species in the field (FIEDLER, 1991). *L. niger* ants are omnivorous ; they feed on insect prey and collect honeydew or similar energy-rich fluids. *Lasius flavus* (Fabricius, 1781) is also very common and lives largely subterranean in European grasslands. Its diet consists almost entirely of honeydew produced by root aphids. Because of their subterranean life, *L. flavus* ants rarely tend lycaenid larvae in nature, but they readily show trophobiotic interactions with lycaenid immatures in the laboratory (FIEDLER, 1991). Ant colonies were kept in the laboratory (at 22-26° C) in earth nests (*L. flavus*), or in artificial nest chambers the bottom of which consisted of plaster of Paris (*L. niger*). Ants were fed with honey-water and dead insects (mostly cockroaches) as needed.

Experiments

Experiments started at the beginning of the third larval instar, when the myrmecophilous glands of *P. icarus*, *P. bellargus* and *A. agestis* become functional. Experimental caterpillars were reared singly in translucent plastic vials (125 ml) equipped as above and were randomly subjected to one of the 4 following treatments : kept with 5 *L. flavus* workers ; with 2 *L. flavus* workers ; with 2 *L. niger* workers ; and controls reared without ants. Food and filter paper were exchanged daily, and the entire larval frass was collected. Ants that had died during the experiment were replaced by nestmates to ensure a constant number of tending ants throughout. The procedure continued during the pupal stage. Daily inspections of every individual larva and pupa confirmed that all immatures of the 3 myrmecophilous species were constantly tended by their ant guard. In the 2 *Lycaena* species, ant-associations were likewise regularly observed, although occasionally larvae were seen without tending ants for short periods of time. Each experiment lasted until the adult butterfly eclosed from the pupa. All individuals that died prior to eclosion were discarded from the analyses. Mortality rates did not differ between the ant treatments within each species (SAAM, 1993). In total, 358 butterflies were reared to maturity (see SAAM, 1993 for further details).

Every individual was weighed 5 times : at the beginning of the experiment (freshly moulted L3 : initial larval weight) ; as immobile nonfeeding prepupa within a few hours prior to pupation (prepupal weight) ; as freshly moulted pupa (initial pupal weight) ; as fully pigmented pupa within 6 h before eclosion ; and as freshly eclosed adult after emission of the meconium (adult weight). The whole frass production over the third and fourth larval instar was collected, dried in an oven at 65°C to constant weight, and then weighed. All weights were recorded to the nearest 0.1 mg using an electronic Sartorius BA 61 balance. In addition, the durations of the third plus fourth larval instars and of the pupal stage were recorded (in days).

From these data the following additional parameters were calculated :

PERCENT PUPAL WEIGHT LOSS : (Initial pupal weight – final pupal weight) × 100 / (initial pupal weight). Pupal weight losses always occur during development, but could be enhanced by the delivery of pupal secretions (e.g. from pore cupola organs) to ants.

RELATIVE GROWTH RATE : RGR = (mass gained in the third plus fourth larval instar) / (prepupal weight × larval duration).

The ratio : (larval mass gain) / (total frass production). This is a rough estimate for the efficiency of the conversion of ingested food into biomass. Assuming that the digestibility of food is not affected by the presence of ants (see Baylis & Pierce, 1992), frass production is proportional to food consumption, if food quality is kept constant.

The data were analysed statistically using ANOVA (with sex and treatment as factors) for multiple comparisons, and Mann-Whitney U-tests for comparisons between pairs of samples where normality or homogeneity of variances were not met (Sachs, 1992). Percent data were arcsine-transformed prior to analysis. All P values given refer to 2-tailed tests.

Results

Duration of larval and pupal development

The duration of the third plus fourth instar (Table 1) was largely unaffected by the presence of ants in *A. agestis* (mean values per experimental series 6-9 d), *P. icarus* (10-12 d), *P. bellargus* (16-23 d), *L. phlaeas* (8-10 d) and *L. tityrus* (11-15 d). Sex differences in the duration of larval development occurred in all 5 species and in almost all treatments. Females generally took 1-2 d longer than males until pupation, but this difference was less distinct in experiments with *P. icarus* and *L. phlaeas.*

The duration of the pupal stage was likewise not influenced by ant-association in all 5 lycaenid species tested. Sex differences in pupal duration were minimal (males faster in *L. tityrus* and *P. bellargus*). The pupal stage of *A. agestis*, *L. phlaeas* and *L. tityrus* took 7-8 d, that of *P. icarus* 9-10 d, and in *P. bellargus* pupal development lasted 11-13 d under the rearing conditions.

Prepupal weights (Table 2)

Caterpillar mass at the end of the larval stage was independent of ant-association in *A. agestis* (means 71-82 mg), *P. bellargus* (means 107-126 mg) and *L. tityrus* (118-127 mg). *P. icarus* males reared in the presence of ants (94.55 ± 1.33 mg) were consistently heavier than control males (89.46 ± 5.44 mg), although the difference was not significant. However, ant-association fostered a sex difference in *P. icarus.* Males reared in the presence of ants were significantly heavier than females ($U_{23;31} = 195$; $Z = 2.825$; $P < 0.01$), whereas control males and females reached equal prepupal weights ($U_{7;13} = 45$; $P > 0.5$). A similar pattern occurred in *L. phlaeas.* Male prepupae reared in association with ants (89.6 ± 3.05 mg) were significantly heavier than controls (73.8 ± 2.34 mg ; $U_{10;24} = 38$; $Z = 3.099$; $P < 0.01$),

Table 1

Duration of larval development (third plus fourth instar, in days) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants. Given are means ± standard errors (sample sizes in brackets). F values are from two-way ANOVA. $^{+}$ P < 0.1 ; * P < 0.05 ; ** P < 0.01 ; *** P < 0.001 ; ns P > 0.10.

Species	5 *Lasius flavus*	2 *Lasius flavus*	2 *Lasius niger*	Without ants	Effect	Ant treatments combined	Effect
Aricia agestis							
Females	8.07 ± 0.36 (15)	8.29 ± 0.33 (17)	9.14 ± 0.34 (7)	8.53 ± 0.30 (17)	treatment : F = 2.14 ns sex : F = 13.91***	8.36 ± 0.21 (39)	ants : F = 0.74 ns sex : F = 8.07**
Males	6.86 ± 0.40 (7)	7.56 ± 0.29 (9)	7.71 ± 0.36 (7)	7.75 ± 0.45 (8)		7.39 ± 0.21 (23)	
Polyommatus icarus							
Females	11.50 ± 0.42 (8)	11.75 ± 0.31 (8)	11.50 ± 0.67 (6)	11.62 ± 0.45 (13)	treatment : F = 0.37 ns sex : F = 2.92^{+}	11.59 ± 0.25 (22)	ants : F = 0.94 ns sex : F = 1.06 ns
Males	11.00 ± 0.24 (11)	10.63 ± 0.42 (8)	11.17 ± 0.32 (12)	11.57 ± 0.37 (7)		10.97 ± 0.18 (31)	
Polyommatus bellargus							
Females	21.17 ± 1.47 (6)	20.50 ± 1.16 (8)	19.14 ± 0.70 (7)	22.50 ± 1.21 (8)	treatment : F = 3.91* sex : F = 4.06*	20.24 ± 0.65 (21)	ants : F = 2.68 ns sex : F = 5.38*
Males	19.00 ± 0.93 (8)	16.50 ± 1.33 (4)	20.00 ± 1.16 (4)	19.57 ± 1.67 (7)		18.63 ± 0.68 (16)	
Lycaena phlaeas							
Females	9.57 ± 0.53 (7)	9.22 ± 0.22 (9)	9.27 ± 0.24 (11)	8.40 ± 0.40 (5)	treatment : F = 1.30 ns sex : F = 4.11*	9.33 ± 0.18 (27)	ants : F = 2.03 ns sex : F = 0.34 ns
Males	8.72 ± 0.27 (11)	8.33 ± 0.31 (7)	8.83 ± 0.17 (6)	8.80 ± 0.29 (10)		8.63 ± 0.16 (24)	
Lycaena tityrus							
Females	12.57 ± 0.84 (7)	14.67 ± 0.76 (6)	13.89 ± 0.77 (9)	13.43 ± 0.68 (7)	treatment : F = 0.71 ns sex : F = 16.83***	13.68 ± 0.48 (22)	ants : F = 0.54 ns sex : F = 13.61***
Males	11.92 ± 0.57 (13)	11.43 ± 0.68 (7)	12.00 ± 0.71 (8)	11.27 ± 0.38 (11)		11.82 ± 0.36 (28)	

Table 2

Final larval weights (in prepupal stage, mg wet weight) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants. Given are means ± standard errors (sample sizes in brackets). F values are from two-way ANOVA. * $P < 0.05$; ** $P < 0.01$; ns $P > 0.10$.

Species	5 *Lasius flavus*	2 *Lasius flavus*	2 *Lasius niger*	Without ants	Effect	Ant treatments combined	Effect
Aricia agestis							
Females	76.02 ± 2.04 (17)	80.10 ± 2.19 (18)	81.81 ± 5.40 (7)	77.47 ± 1.75 (19)	treatment : F = 0.05 ns sex : F = 7.76**	78.74 ± 1.59 (42)	ants : F = 0.01 ns sex : F = 4.63*
Males	76.56 ± 2.49 (8)	71.42 ± 2.03 (10)	71.51 ± 3.22 (7)	73.98 ± 2.71 (9)		73.09 ± 1.47 (25)	
Polyommatus icarus							
Females	89.63 ± 2.51 (8)	88.13 ± 2.38 (8)	86.21 ± 3.70 (7)	89.19 ± 2.73 (13)	treatment : F = 0.29 ns sex : F = 5.16*	88.07 ± 1.60 (23)	ants : F = 0.70 ns sex : F = 2.02 ns
Males	92.63 ± 2.23 (11)	92.40 ± 2.05 (8)	97.73 ± 2.25 (12)	89.46 ± 5.44 (7)		94.55 ± 1.33 (31)	
Polyommatus bellargus							
Females	106.52 ± 6.55 (6)	109.63 ± 4.24 (8)	112.10 ± 4.46 (7)	113.69 ± 5.76 (8)	treatment : F = 1.15 ns sex : F = 8.08**	109.56 ± 2.77 (21)	ants : F = 1.99 ns sex : F = 7.80**
Males	117.83 ± 1.88 (8)	115.48 ± 8.43 (4)	125.23 ± 5.18 (4)	126.07 ± 5.24 (7)		119.12 ± 2.58 (16)	
Lycaena phlaeas							
Females	89.67 ± 4.84 (7)	98.70 ± 6.37 (9)	90.64 ± 4.49 (11)	83.42 ± 8.39 (6)	treatment : F = 3.08* sex : F = 1.45 ns	93.07 ± 3.06 (27)	ants : F = 8.28** sex : F = 2.19 ns
Males	88.24 ± 5.50 (11)	85.50 ± 5.56 (7)	93.50 ± 2.87 (6)	73.80 ± 2.34 (10)		89.60 ± 3.05 (24)	
Lycaena tityrus							
Females	118.11 ± 6.77 (7)	127.00 ± 4.98 (6)	126.01 ± 5.77 (9)	121.27 ± 7.59 (7)	treatment : F = 0.58 ns sex : F = 0.22 ns	123.77 ± 3.42 (22)	ants : F = 0.05 ns sex : F = 0.09 ns
Males	119.23 ± 3.61 (13)	119.37 ± 4.76 (7)	125.13 ± 3.86 (8)	121.56 ± 5.01 (11)		120.95 ± 2.30 (28)	

whereas females showed no effect (mean weights 83.42 ± 8.39 mg and 93.07 ± 3.06 mg ; $U_{6;27} = 51$; $Z = 1.40$; $P = 0.17$).

A general sex difference in prepupal weights emerged only in 2 species. *A. agestis* males were smaller than females, in *P. bellargus* males were larger. In *P. icarus* and *L. phlaeas*, the sex difference was only apparent in ant-tended individuals (males larger than females, see above). Females and males of *L. tityrus* reached similar prepupal weights. Significant statistical ant-sex interactions were not observed.

Pupal weight loss

In all 5 species, ant-association had no detectable influence on pupal weight loss. Mean weight losses accounted for 15-20% in *A. agestis, P. icarus* and *L. phlaeas*, but were slightly higher in *L. tityrus* (> 20% in females) and highest in *P. bellargus* (average values per series 23-28%). Sex differences in pupal weight loss were distinct only in *L. tityrus* (female pupae lost more weight [22-24% on average] than males [average loss 17-19%]). Otherwise, there were neither sex differences nor significant ant-sex interactions.

Adult weights (Table 3)

Adult weights were not affected by ant-association in *A. agestis, P. bellargus* and *L. tityrus*. In *P. icarus*, ant-tended males (35.07 ± 0.76 mg) were ca. 10% heavier than untended controls (31.27 ± 1.21 mg ; $U_{7;31} = 50$; $Z = 2.20$; $P < 0.02$), whereas females showed no effect (ant-sex interaction : $F_{1;67} = 3.92$; $P < 0.05$). A similar effect was observed in *L. phlaeas* : ant-tended individuals (especially males : 31.41 ± 1.70 mg) eclosed from the pupae at higher weights than untended controls (23.65 ± 0.85 mg). As a consequence, there was no significant sex difference in adult weights of ant-tended *P. icarus* and *L. phlaeas*, whereas untended controls of both species showed a distinct size dimorphism (females heavier than males). In *A. agestis* there was a significant sex difference independent of ant-association, females being heavier than males. No significant size dimorphism occurred in *P. bellargus* and *L. tityrus.*

Growth rates (Table 4)

In all 5 species tested, males tended to grow faster than females. This difference was only weakly developed in *P. icarus* and *L. phlaeas*, but was pronounced in the remaining 3 species. Only in *A. agestis* was there a weak trend that caterpillars in association with 5 *Lasius flavus* ants grew slightly faster than all others. In all, ant-association had no

Table 3

Adult weights (mg wet weight) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants.
Given are means ± standard errors (sample sizes in brackets).
F values are from two-way ANOVA. $^+$ $P < 0.1$; * $P < 0.05$; *** $P < 0.001$; ns $P > 0.10$.

Species	5 *Lasius flavus*	2 *Lasius flavus*	2 *Lasius niger*	Without ants	Effect	Ant treatments combined	Effect
Aricia agestis							
Females	30.72 ± 1.22 (17)	30.66 ± 1.29 (18)	35.96 ± 3.38 (7)	31.24 ± 1.28 (19)	treatment : F = 0.65 ns sex : F = 38.76***	31.57 ± 0.95 (42)	ants : F = 0.01 ns sex : F = 29.34***
Males	26.13 ± 0.97 (8)	25.21 ± 0.69 (10)	24.01 ± 1.05 (7)	25.51 ± 1.14 (9)		25.17 ± 0.51 (25)	
Polyommatus icarus							
Females	36.54 ± 1.28 (7)	35.26 ± 0.94 (8)	33.34 ± 0.89 (5)	35.94 ± 1.57 (13)	treatment : F = 1.04 ns sex : F = 1.20 ns	35.23 ± 0.65 (20)	ants : F = 1.84 ns sex : F = 4.49*
Males	35.41 ± 1.40 (11)	35.01 ± 1.13 (8)	34.80 ± 1.38 (12)	31.27 ± 1.21 (7)		35.07 ± 0.76 (31)	
Polyommatus bellargus							
Females	35.42 ± 4.47 (6)	41.48 ± 3.22 (8)	38.00 ± 2.30 (7)	41.60 ± 2.93 (8)	treatment : F = 0.37 ns sex : F = 1.01 ns	38.59 ± 1.91 (21)	ants : F = 0.83 ns sex : F = 0.68 ns
Males	42.04 ± 3.51 (8)	38.23 ± 3.28 (4)	43.22 ± 4.32 (4)	43.20 ± 3.38 (7)		41.38 ± 2.14 (16)	
Lycaena phlaeas							
Females	31.09 ± 2.67 (7)	37.30 ± 4.22 (8)	32.23 ± 2.32 (11)	30.27 ± 3.00 (6)	treatment : F = 2.15 ns sex : F = 2.57 ns	33.48 ± 1.77 (26)	ants : F = 5.49* sex : F = 3.43$^+$
Males	31.63 ± 3.23 (11)	31.08 ± 2.44 (6)	31.35 ± 2.14 (6)	23.65 ± 0.85 (10)		31.41 ± 1.70 (23)	
Lycaena tityrus							
Females	40.52 ± 2.18 (7)	46.42 ± 2.60 (6)	47.56 ± 3.06 (9)	44.06 ± 3.50 (7)	treatment : F = 1.25 ns sex : F = 1.67 ns	45.22 ± 1.72 (21)	ants : F = 0.01 ns sex : F = 1.48 ns
Males	39.89 ± 2.64 (13)	41.13 ± 2.45 (7)	44.37 ± 3.52 (7)	42.18 ± 2.34 (11)		41.37 ± 1.67 (27)	

Table 4

Relative growth rates (in mg/mg * d) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants. Given are means ± standard errors (sample sizes in brackets). F values are from two-way ANOVA. $^{+}$ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns $P > 0.10$.

Species	5 *Lasius flavus*	2 *Lasius flavus*	2 *Lasius niger*	Without ants	Effect	Ant treatments combined	Effect
Aricia agestis							
Females	0.114 ± 0.004 (17)	0.111 ± 0.003 (18)	0.104 ± 0.003 (7)	0.108 ± 0.003 (19)	treatment : F = 2.58^{+}	0.111 ± 0.002 (42)	ants : F = 1.46 ns
Males	0.130 ± 0.005 (8)	0.119 ± 0.005 (10)	0.118 ± 0.004 (7)	0.117 ± 0.005 (9)	sex : F = 14.77***	0.122 ± 0.003 (25)	sex : F = 9.56**
Polyommatus icarus							
Females	0.085 ± 0.003 (8)	0.083 ± 0.002 (8)	0.086 ± 0.004 (7)	0.084 ± 0.003 (13)	treatment : F = 0.59 ns	0.085 ± 0.002 (23)	ants : F = 1.72 ns
Males	0.089 ± 0.002 (11)	0.091 ± 0.003 (8)	0.088 ± 0.003 (12)	0.084 ± 0.003 (7)	sex : F = 3.30^{+}	0.089 ± 0.001 (31)	sex : F = 1.20 ns
Polyommatus bellargus							
Females	0.046 ± 0.003 (6)	0.047 ± 0.002 (8)	0.051 ± 0.002 (7)	0.043 ± 0.002 (8)	treatment : F = 1.81 ns	0.048 ± 0.001 (21)	ants : F = 2.30 ns
Males	0.051 ± 0.002 (8)	0.059 ± 0.005 (4)	0.048 ± 0.003 (4)	0.050 ± 0.004 (7)	sex : F = 6.30*	0.052 ± 0.002 (16)	sex : F = 5.78*
Lycaena phlaeas							
Females	0.102 ± 0.005 (7)	0.105 ± 0.003 (9)	0.105 ± 0.003 (11)	0.106 ± 0.011 (6)	treatment : F = 1.07 ns	0.104 ± 0.002 (27)	ants : F = 0.04 ns
Males	0.111 ± 0.004 (11)	0.116 ± 0.005 (7)	0.110 ± 0.002 (6)	0.110 ± 0.003 (10)	sex : F = 3.77^{+}	0.113 ± 0.002 (24)	sex : F = 2.92^{+}
Lycaena tityrus							
Females	0.079 ± 0.005 (7)	0.068 ± 0.004 (6)	0.072 ± 0.004 (9)	0.074 ± 0.004 (7)	treatment : F = 0.58 ns	0.073 ± 0.003 (22)	ants : F = 0.27 ns
Males	0.084 ± 0.004 (13)	0.086 ± 0.005 (7)	0.083 ± 0.004 (8)	0.087 ± 0.002 (11)	sex : F = 17.15***	0.084 ± 0.002 (28)	sex : F = 14.21***

Table 5

Ratio of larval mass gain and frass production (mg wet weight/mg dry weight) of five European Lycaenidae species when reared in the presence or absence of *Lasius* ants. Given are means ± standard errors (sample sizes in brackets). F values are from two-way ANOVA. $^+$ $P < 0.1$; * $P < 0.05$; ns $P > 0.10$.

Species	5 *Lasius flavus*	2 *Lasius flavus*	2 *Lasius niger*	Without ants	Effect	Ant treatments combined	Effect
Aricia agestis							
Females	1.51 ± 0.10 (17)	1.46 ± 0.08 (18)	1.69 ± 0.11 (7)	1.34 ± 0.06 (19)	treatment : F = 2.07 ns sex : F = 1.10 ns	1.52 ± 0.06 (42)	ants : F = 3.69$^+$ sex : F = 0.22 ns
Males	1.49 ± 0.08 (8)	1.41 ± 0.08 (10)	1.46 ± 0.08 (7)	1.34 ± 0.11 (9)		1.45 ± 0.05 (25)	
Polyommatus icarus							
Females	1.70 ± 0.07 (8)	1.78 ± 0.22 (8)	1.82 ± 0.25 (7)	1.81 ± 0.09 (13)	treatment : F = 0.38 ns sex : F = 4.21*	1.76 ± 0.10 (23)	ants : F = 0.23 ns sex : F = 2.34 ns
Males	2.04 ± 0.15 (11)	1.91 ± 0.18 (8)	2.15 ± 0.12 (12)	1.89 ± 0.06 (7)		2.05 ± 0.08 (31)	
Polyommatus bellargus							
Females	1.88 ± 0.14 (6)	1.75 ± 0.08 (8)	1.45 ± 0.07 (7)	1.94 ± 0.10 (8)	treatment : F = 3.91* sex : F = 4.06*	1.68 ± 0.07 (21)	ants : F = 3.85$^+$ sex : F = 2.63 ns
Males	1.90 ± 0.12 (8)	2.10 ± 0.19 (4)	1.71 ± 0.21 (4)	2.06 ± 0.16 (7)		1.90 ± 0.09 (16)	
Lycaena phlaeas							
Females	3.97 ± 0.31 (7)	3.98 ± 0.38 (9)	4.62 ± 0.30 (11)	3.64 ± 0.26 (6)	treatment : F = 0.95 ns sex : F = 0.67 ns	4.23 ± 0.19 (27)	ants : F = 0.91 ns sex : F = 0.86 ns
Males	3.96 ± 0.28 (11)	4.97 ± 0.66 (6)	3.92 ± 0.21 (5)	4.22 ± 0.36 (10)		4.22 ± 0.24 (22)	
Lycaena tityrus							
Females	3.47 ± 0.36 (7)	3.87 ± 0.24 (6)	3.58 ± 0.22 (9)	3.53 ± 0.14 (7)	treatment : F = 1.51 ns sex : F = 2.77$^+$	3.62 ± 0.16 (22)	ants : F = 4.36* sex : F = 0.58 ns
Males	4.31 ± 0.33 (13)	4.25 ± 0.39 (7)	4.08 ± 0.34 (8)	3.30 ± 0.24 (11)		4.23 ± 0.20 (28)	

significant influence on growth rates. Relative growth rates (daily mass gain divided by prepupal mass) were 0.10-0.13 mg/mg * d in *A. agestis* and *L. phlaeas*, 0.07-0.09 mg/mg * d in *P. icarus* and *L. tityrus*, and 0.045-0.05 mg/mg * d in *P. bellargus*.

Frass production and efficiency of food conversion (Table 5)

The ratio of larval mass gain (wet weight) and frass production (dry weight) was at most weakly affected by ant-association in all 5 species. In *P. bellargus*, this ratio was lower in the experimental series with 2 *L. niger* ants. This series was reared later in the season than all others, and the differences most likely indicate a change in hostplant quality rather than any influence of ant-tending. In *A. agestis*, *L. phlaeas* and *L. tityrus*, no consistent effects of ants were found. For *P. icarus*, ANOVA indicated no influence of ant-association on food utilization. However, ant-tended males had a significantly higher mass gain/frass ratio than ant-tended females ($U_{23;31} = 170$; $Z = 3.26$; $P < 0.002$), whereas in control experiments this sex difference did not occur ($U_{7;13} = 34$; $P > 0.2$). Overall, sex differences in this parameter were minimal, and average values for the treatments ranged from 1.34-1.52 mg/mg in *A. agestis*, 1.70-2.05 mg/mg in both *Polyommatus* species, and 3.30-4.97 mg/mg in the two *Lycaena* species.

Discussion

Differences in developmental parameters between males and females were observed in all 5 species tested. Generally males developed faster (shorter larval period, higher growth rate). This is in accordance with the protandry of all 5 species in nature.

All species examined produce 2 or more generations per year in central or southern Europe. The most rapid development was observed in *A. agestis* and *L. phlaeas*. These two species produce 3-4 generations per year in central Europe in favourable seasons. *P. icarus* was somewhat slower (2-3 generations per year), and *L. tityrus* as well as *P. bellargus* took longest to reach maturity. In the latter two species a third generation is a very rare exception north of the Alps (EBERT & RENNWALD, 1991). Thus, our laboratory results are consistent with phenological observations made in the field.

Pupal weight losses were highest in *P. bellargus*, the species with the longest pupal stage, and were fairly similar among the remaining 4 species. Concerning the ratio of mass gain per frass production, the two myrmecoxenous *Lycaena* species far surpassed the 3 myrmecophilous members of the *Polyommatus* group. Both *Lycaena* species feed on leaves of *Rumex* species (Polygonaceae). These leaves appear to have a lower content of undigestible material than the legume hostplants of *P. icarus* or *P. bellargus*. PIERCE (1985) has argued that myrmecophily has selected for the utilization of nutrient-rich hostplants (especially nitrogen-rich legumes and inflorescences), but obviously the 2 *Lycaena* species perform in a superior manner on the foliage of a non-legume host. According to its biomass/frass ratio, *A. agestis* utilizes the poorest hostplant material (leaves of Geraniaceae), but nevertheless the caterpillars are highly myrmecophilous. The nutritional constraints on larval myrmecophily are a rewarding field open to further investigation (BAYLIS & PIERCE, 1993).

Overall, ants had very little impact on the developmental parameters studied, and the few marginally significant ant-effects which could be detected were mostly beneficial. From facultatively myrmecophilous Lycaenidae butterflies like *Polyommatus icarus* or *Hemiargus isola* it is already known that ant-association does not necessarily pose developmental costs, but may even allow overcompensation of the investment into myrmecophily (FIEDLER & HÖLLDOBLER, 1992 ; WAGNER, 1993). Our present data fully corroborate that pattern.

Aricia agestis and *Polyommatus bellargus* are both facultative myrmecophiles whose older larvae are almost never found without tending ants (e.g. THOMAS & LEWINGTON, 1991). In these species, ant-association had very limited effects on developmental parameters, suggesting that larvae of both sexes can fully compensate for the costs of myrmecophily. In recent experiments with *A. agestis*, we could even demonstrate a beneficial effect of ant-attendance on prepupal weights (tended individuals are ca. 10% heavier, but develop more slowly : Hummel & Fiedler, unpublished). *Polyommatus icarus* is a facultative myrmecophile with a rather loose relationship to ants (THOMAS & LEWINGTON, 1991). Caterpillars of this species produce less secretion from their nectar organs than *P. coridon* and its close relatives (FIEDLER, 1991), suggesting a comparatively low energetic investment into myrmecophily. Our experimental data confirm the findings of FIEDLER & HÖLLDOBLER (1992) that ant-tended *P. icarus* males grow larger than untended controls, whereas tended females appear to fully compensate for their costs of myrmecophily.

Weak male-limited benefits also occurred in myrmecoxenous *Lycaena* species (weight in *L. phlaeas*, food conversion in *L. tityrus*). Caterpillars of both species lack a dorsal nectar organ. Accordingly, their energetic investment in interactions with ants must be low (only through the ubiquitous pore cupola organs). Ant-associations of these species are unknown in the wild, but under laboratory conditions weak and unstable associations can be induced (Fiedler, 1991).

As in the case of certain ant-tended aphids which show better growth in the presence of ants (Banks & Nixon, 1958), the physiological mechanisms responsible for overcompensation in some lycaenid caterpillars remain unclear. Ant-tended caterpillars did not produce more frass than untended controls (Saam, 1993). Therefore, total food consumption was probably equal between the groups. Rather, the efficiency of food conversion into biomass may be stimulated by tending ants. Circumstantial evidence for this hypothesis was found in *A. agestis*, *P. icarus* and *L. tityrus*, where ant-tended individuals showed enhanced conversion of food.

Alternatively, the stimulation of caterpillars could be a predominantly behavioural phenomenon (see discussion in Wagner, 1993). Perhaps feeding behaviour is less often interrupted in ant-tended individuals, facilitating a more effective food utilization. Caterpillars of *P. icarus*, *P. coridon* and other myrmecophilous species resume locomotion and feeding more rapidly after experimental disturbance when ants are present (Fiedler, unpublished). In the Nearctic *Glaucopsyche lygdamus* (Doubleday, 1841), untended caterpillars are much more likely to drop off the hostplant (Pierce & Easteal, 1986). Developmental effects of ant-attendance have not been studied in detail in this latter species, but pupal weights of tended and untended individuals did not differ (Pierce & Easteal, 1986).

One could argue that, under the confined conditions of artificial ant-associations, ants do not harvest larval secretions as eagerly as they would do if they could transfer their crop content to their colony. Three lines of evidence contradict this view. Firstly, caterpillars and pupae of all 5 species tested were regularly tended by ants (and the 3 myrmecophilous species constantly so) throughout the whole experimental period. Tending levels did not decrease with time. This indicates that the ants, which had no access to alternative food sources, exerted a permanent pressure on the lycaenid immatures to deliver their secretions. Secondly, in *P. icarus* (and in the myrmecoxenes *L. phlaeas* and *L. tityrus*) the numbers of ants per larva used in our experiments were comparable to, or even higher than, the average number of tending ants observed so far in nature. Hence, at least in these species compensation or overcompensation occurred despite a relatively high level of ant-attendance.

Thirdly, the amounts of nectar secretion produced by single lycaenid larvae over the third plus fourth instar are sufficiently small to be sampled completely by a small number of ant workers. In *P. icarus* and *A. agestis*, for example, individual lifetime nectar secretion volumes amount to 10 µl or less, equivalent to approximately 1.5 mg carbohydrates at most (Fiedler, Burghardt & Hummel, unpublished). However, we cannot rule out the possibility that in future experiments (e.g. with higher tending levels or involving other ant species) deviating results could be obtained. The actual outcome of potentially mutualistic interspecific interactions can be strongly shaped by environmental conditions such as hostplant quality or density of interacting species (CUSHMAN & WHITHAM, 1991 ; BRETON & ADDICOTT, 1992).

There is steadily increasing evidence that compensation or even overcompensation of the energetic costs resulting from ant-association is not uncommon among facultatively myrmecophilous lycaenid butterflies. This finding could explain why facultative, and sometimes weak, interactions with ants are so common and taxonomically widespread across the diversity of Lycaenidae butterflies (FIEDLER, 1991). If myrmecophily were generally a high-cost strategy under severe selective regimes, one would have to expect strong disruptive selection favouring either close and obligatory myrmecophily with high costs, but high rewards for the lycaenids, or favouring the reduction of myrmecophily. In contrast to this expectation, facultative ant-associations appear to be more common in lycaenid butterflies than cases of obligatory myrmecophily (PIERCE, 1987 ; FIEDLER, 1991). Many examples of facultative interactions with ants are probably best described as low-cost mutualisms, where the lifetime energetic investment of individual caterpillars accounts for a few µl of secretions. It is then not surprising that myrmecophily is an evolutionarily rather stable component in the life-history of so many Lycaenidae species.

A broad continuum of cost-benefit relationships in terms of myrmecophily does exist across the diversity of Lycaenidae butterflies. This is reflected by the variety of developmental effects these ant-association can have in various lycaenid species, ranging from severe costs to substantial benefits. In general, the developmental costs for the larvae appear to parallel the degree of obligateness of the ant-lycaenid associations : the more dependent the larvae are on ants, the higher the costs the ants can in turn impose. Further comparative studies on species representing various taxonomic groups and different types of myrmecophily will strengthen our ecological and evolutionary understanding of lycaenid-ant interactions.

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Oviposition behaviour in *Lycaena thetis* Klug (Lepidoptera : Lycaenidae)

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Summary

The oviposition behaviour of *Lycaena thetis* was observed in the Aladag mountains, southern Turkey. Females drop their eggs singly into the spiny cushions of the larval foodplant (*Acantholimon* spp., Plumbaginaceae).

Zusammenfassung

Das Eiablageverhalten von *Lycaena thetis* wurde im Aladag-Gebirge (Süd-Türkei) beobachtet. Die Weibchen lassen ihre Eier einzeln in die dornigen Kugelpolster ihrer Wirtspflanze (*Acantholimon* spp., Plumbaginaceae) fallen.

The life histories of European or North American species of the Lycaenini ("Copper butterflies") are, in general, well known. For most Asian *Lycaena* Fabricius, 1807, species, however, even basic biological information on hostplants, voltinism, or diapause stages is lacking (cf. Fiedler, 1991). Recently, Tolman (1993) published a detailed account of the larval biology of *Lycaena thetis* Klug, 1834, from southern Greece. Since Tolman based his description on field-collected young, hibernated larvae, the oviposition behaviour of *L. thetis* remained unknown. Furthermore, Tolman's paper deals with the westernmost populations of *L. thetis*. Because the distribution of *L. thetis* extends throughout Asia Minor to northern Iran (Schurian & Hofmann, 1982), it remained to be tested whether populations in the heart of the species' range utilize the same or similar hostplants.

On 15.viii.1993, between 11.00-15.00 EEST, we had the opportunity to observe the unusual oviposition behaviour of *L. thetis* in a population of southern Turkey. The habitat was a south-facing steep slope in a valley of the Aladag mountains (Prov. Nidge), approximately 1800-

1900 m above sea level. This slope was mostly covered by limestone boulders and scree. The sparse vegetation contained *Juniperus* shrubs and single conifer trees. Spiny, cushion-forming, perennial plants (*Astragalus* and *Acantholimon* spp.) which are relatively immune to overgrazing by the abundant sheep and goats, formed the lower vegetation between the boulders.

Fig. 1. Large contiguous cushions (total diameter > 1 m) of *Acantholimon* sp. (Plumbaginaceae), the hostplant of *Lycaena thetis*.

When we first walked through the habitat late in the morning, only few territorial males and nectaring females of *L. thetis* were on the wing. Males preferably basked on barren ground. Around noon, when the air temperatures had reached about 30°C, females became increasingly active. They often visited the last flowers of *Acantholimon* spp. (Plumbaginaceae). This cushion plant with extremely spiny, needle-like leaves (Fig. 1) is the hostplant of *L. thetis* in Greece (Tolman, 1993), although we were unaware of his paper at the time of our observations. Females examined the *Acantholimon* cushions in the fluttery searching flights that typically precede oviposition in many lycaenid butterflies. After alighting, each female would crawl about on the cushions for several minutes, repeatedly curling its abdomen and probing the plant surface with the antennae and ovipositor. However, despite intensive close examination of the respective plants after the females had flown off, we failed to find any eggs attached to the twigs or leaves.

Finally, we succeeded in observing the actual oviposition act. When viewed in contre-jour, we could clearly see that after up to 5 minutes of intensive crawling and probing the hostplant, the female eventually inserts its ovipositor between the needle-like leaves and simply drops a single egg into the cushion. In one case, the egg by chance stuck to a twig deep within an *Acantholimon* cushion, but unfortunately it fell to the ground during our attempt to secure it. The hemispherical egg was rather large (ca. 1 mm in diameter) and showed the rough chorionic sculpturing typical for *Lycaena* eggs. In total, we observed 10 successful oviposition acts, all in the same manner. On at least twice as many occasions, a female left the hostplant without laying an egg.

Ovipositions only occurred during the hottest hours around noon. When we left the habitat (15.00), the females tended to bask for long periods on the *Acantholimon* cushions, and flight activity evidently decreased. We followed various individual females for dozens of metres. These females ignored many potential hostplant cushions and alighted to probe quite a number of *Acantholimon* plants before an egg was laid. Hence, they appear to be very choosy, but we do not know the factors that finally elicit oviposition. Egg-laying occurred on small as well as on large plants (Ø = 30-100 cm) and not invariably in full sun, although high temperatures are clearly required. All eggs were dropped into the central part of a cushion, not at the edges.

To obtain oviposition in captivity, we collected a total of 10 females from various habitats in southern Turkey in August 1993. These were caged in a plastic bottle (1.5 l) lined with moist filter paper, twigs of the hostplant *Acantholimon* as oviposition substrate, and sugar solution as food. However, despite exposing the females to various conditions (direct sunlight, shadow, high temperatures, high or low humidity), not a single egg was laid. The last female died after 14 days in captivity. When earlier attempting to obtain eggs from *L. thetis* in captivity (1977 and 1984), females had been confined with an erroneously presumed hostplant (*Rumex* sp., Polygonaceae) without any success. Our failure to induce oviposition in captivity contrasts sharply with successful attempts involving various other Lycaenidae species (*Lycaena candens* (Herrich-Schäffer, 1844), *Agrodiaetus* spp., *Polyommatus* spp.) under similar conditions. Females of *L. thersamon* (Esper, 1784) (like *L. thetis*, often assigned to the "subgenus" *Thersamonia* Verity, 1919), however, laid only few eggs, suggesting that in both species highly xerothermic conditions (and presumably unknown factors) are essential for egg-laying.

Dropping the eggs instead of attaching them onto the hostplant is a very rare behaviour in Lycaenidae butterflies, but has been recorded from the Nearctic *Lycaena rubidus* (Behr, 1866 ; see Funk, 1975). In *L. thetis*, the females may thereby avoid fatal injuries inflicted by the extremely spiny leaves, and the eggs are probably protected against many enemies within the dense thorny *Acantholimon* cushions. It remains to be proven whether *L. thetis* hibernates in the egg stage or whether the larvae hatch in late summer to diapause. Both strategies occur within the genus *Lycaena*. Since Tolman (1993) found larvae of 4-7 mm length shortly after hibernation in Greece, diapause as a young caterpillar seems more likely.

Our observations confirm that *Acantholimon* is the hostplant not only for Greek, but also for Turkish *L. thetis* populations. The plant family Plumbaginaceae is well represented in eremic steppe habitats. In addition, Plumbaginaceae are not too distantly related to the usual Polygonaceae hostplants of most *Lycaena* species (both plant families belong to the subclass Caryophyllidae). Schurian & Hofmann (1982) explicitly mentioned the presence of *Acantholimon* (in part quoted as "*Acantolimnus*") in habitats of *L. eberti* Forster, 1972, and Lukhtanov & Lukhtanov (1994) recorded the hostplant of *L. solskyi* (Erschoff, 1874) as *Acantholimon*. Therefore, additional species of Asian *Lycaena* might also use *Acantholimon* as hostplant. Fuchs (1989) reported that *L. thetis* (especially females) preferably visited another spiny cushion plant, *Drypis spinosa* (Caryophyllaceae), in central Greece for nectaring and basking. Whether this plant species could serve as alternative larval hostplant, needs to be demonstrated.

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Book reviews — Buchbesprechungen — Analyses

Oecophorine Genera of Australia. I. The *Wingia* Group (Lepidoptera : Oecophoridae). Monographs on Australian Lepidoptera, vol. 3. Ian F. B. Common. xvi, 390 pp., 712 Figs. 25.9 × 18.2 cm, hardback. CSIRO Publications, 1994. ISBN 0 643 05524 X. Obtainable from CSIRO Publications, 314 Albert St., East Melbourne, Victoria 3002, Australia, or Apollo Books, Kirkeby Sand 19, DK-5771 Stenstrup, Denmark. Price : $US 100, or $AS 100 in Australia. A discount of 25% is given to subscribers of the series.

The third volume of this major work on the Australian Lepidoptera fauna deals with the genera of the subfamily Oecophorinae. With 1886 valid named species and an estimated species total of more than 5000, the Oecophorinae is by far the best represented group of Lepidoptera in Australia. The wealth of species in Australia is disproportionate, being about 70% of the world fauna. With 170 named genera and an estimated total of 275, clearly all cannot be treated in a single volume. The present volume is the first of three parts and covers the 91 genera of the *Wingia* group. The author is well-known for his excellent book 'Moths of Australia' (see review in *Nota lepid.* 14 (3) : 292).

As in the previous volume, introductory chapters on 'Phylogeny', including a tentative phylogenetic analysis of the subfamily genera, 'Morphology', 'Biology' and 'Diversity and Distribution' are given.

The only synapomorphies of the *Wingia* group are to be found on the abdominal sternum and in the male genitalia. It is not stated however whether an experienced lepidopterist can recognise most species belonging to this group on external characters only. A key to the genera is provided, based on external and internal morphological features. The treatment of each species follows the same format as in the previous volume (for review, see *Nota lepid.* 16 (3/4) : 265-266).

The high scientific quality of the series is maintained in this volume and as such can be highly recommended to students of this family or of the Australian Lepidoptera fauna in general. Unexpectedly, considering the usually high standard of production, in the reviewer's copy the text was bound to the cover upside down !

Steven Whitebread

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Morphology and taxonomy of the species belonging to the genus *Myinodes* Meyrick, 1892 (Lepidoptera : Geometridae)

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Summary

Two new species and one new subspecies of the genus *Myinodes* Meyrick, 1892 are described : *Myinodes interpunctaria atlantica* ssp. n. from Spain, *Myinodes constantina* sp. n. from Algeria and *Myinodes shohami* sp. n. from Jordan. Until recently, the genus was considered to be monotypical, with *M. interpunctaria* (Herrich-Schäffer, 1839) the only known species.

Zusammenfassung

Myinodes interpunctaria (Herrich-Schäffer, 1839) war in der Literatur bisher stets als einzige Art (Typusart) der Gattung *Myinodes* betrachtet worden. Eine genauere morphologische Analyse ergab, daß die aus Nordafrika, Südeuropa und Vorderasien bekannten Populationen einen aus mehreren verschiedenen Arten bestehenden Komplex bilden. In der vorliegenden Arbeit werden zwei neue Arten und eine neue Unterart beschrieben : *Myinodes interpunctaria atlantica* ssp. n. aus Spanien, *Myinodes constantina* sp. n. aus Algerien und *Myinodes shohami* sp. n. aus Jordanien.

Résumé

Description de deux nouvelles espèces et d'une nouvelle sous-espèce du genre *Myinodes* Meyrick, 1892 : *Myinodes interpunctaria atlantica* ssp. n. d'Espagne, *M. constantina* sp. n. d'Algerie et *M. shohami* sp. n. de Jordanie. Jusqu'à tout récemment, ce genre était considéré comme monotypique avec *M. interpunctaria* (Herrich-Schäffer, 1839) comme seule espèce connue.

Until recently, the genus *Myinodes* Meyrick, 1892 was considered to comprise only the species *interpunctaria* (Herrich-Schäffer, 1839). Detailed morphological studies have revealed, however, that the populations known from northern Africa, southern Europe and the Middle East constitute a complex of different species. In this paper two new species and one new subspecies are described : *Myinodes interpunctaria atlantica* ssp. n. from Spain, *Myinodes constantina* sp. n. from Algeria and *Myinodes shohami* sp. n. from Jordan.

Systematic part

Abbreviations :

BUS : Bet Ussishkin Museum, Tel Dan, N.-Israel.
NHMW : Naturhistorisches Museum Wien, Austria.
NLK : Naturkundliche Landessammlungen Karlsruhe, Germany.
TAU : Tel Aviv University Collection, Israel.
ZFMK : Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.
ZSM : Zoologische Staatssammlung München, Germany.

Myinodes Meyrick, 1892

Eusarca Herrich-Schäffer, 1847 (partim)
Pseudotagma Staudinger, 1892
Type species : Sterrha interpunctaria Herrich-Schäffer, 1839 : pl. 6 and wrapper ; by monotypy.

VENATION : Hindwing Sc + R1 and Rs not fused (as in the subfamily Alsophilinae), M2 tubular. Tongue developed, length about 4 mm. Frons strongly convex. Palpi long. Male antennae with two rows of cilia, female antennae simple, finely ciliate beneath. Male and female hindlegs long and slender, with two pairs of long spurs. In the male genitalia uncus developed, often with a subapical lobe ; juxta with caudal excavation ; costal part of valva strongly sclerotized, harpe prominent ; aedoeagus long, slender, with one cornutus, laterally sclerotized (differently in each species). In the female genitalia apophyses weak ; ductus bursae comparatively long and stout ; bursa copulatrix longitudinally ribbed (not in *M. constantina*), without signa, joins ductus bursae laterally on the latter. Ansa of the tympanon apically pointed. In most of these characters very similar to the genus *Eumegethes* Staudinger, 1898.

The systematic position of the genera *Myinodes* and *Eumegethes* is not the subject of this paper, They are usually placed in the subfamily "Oenochrominae" (s.l.). However, they are not closely related with this subfamily (s.str.), which is mainly distributed in SE Asia and Australia, or with the subfamily Alsophilinae.

Myinodes interpunctaria interpunctaria (Herrich-Schäffer, 1839)

Sterrha interpunctaria Herrich-Schäffer, 1839 : pl. 6 and wrapper. Locus typicus : Sicily.

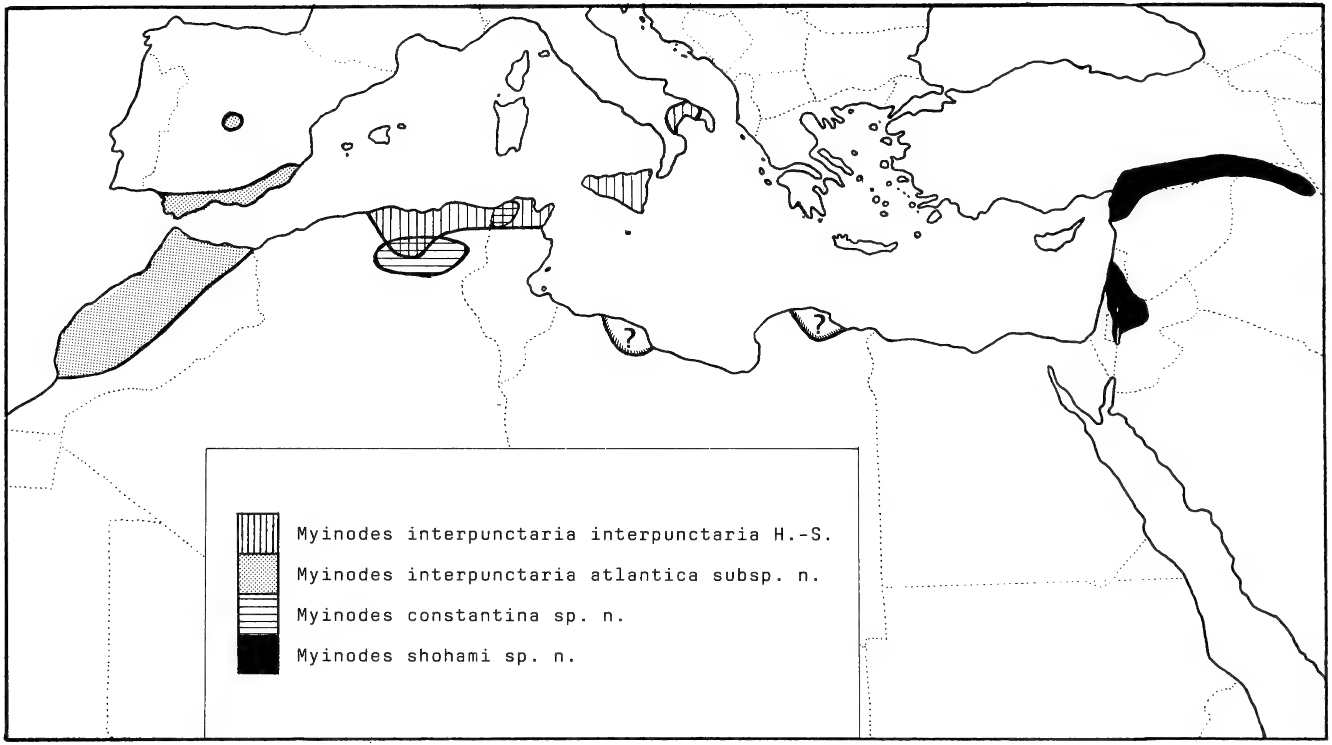


Fig. 1. Distribution of the various taxa of the genus *Myinodes*.

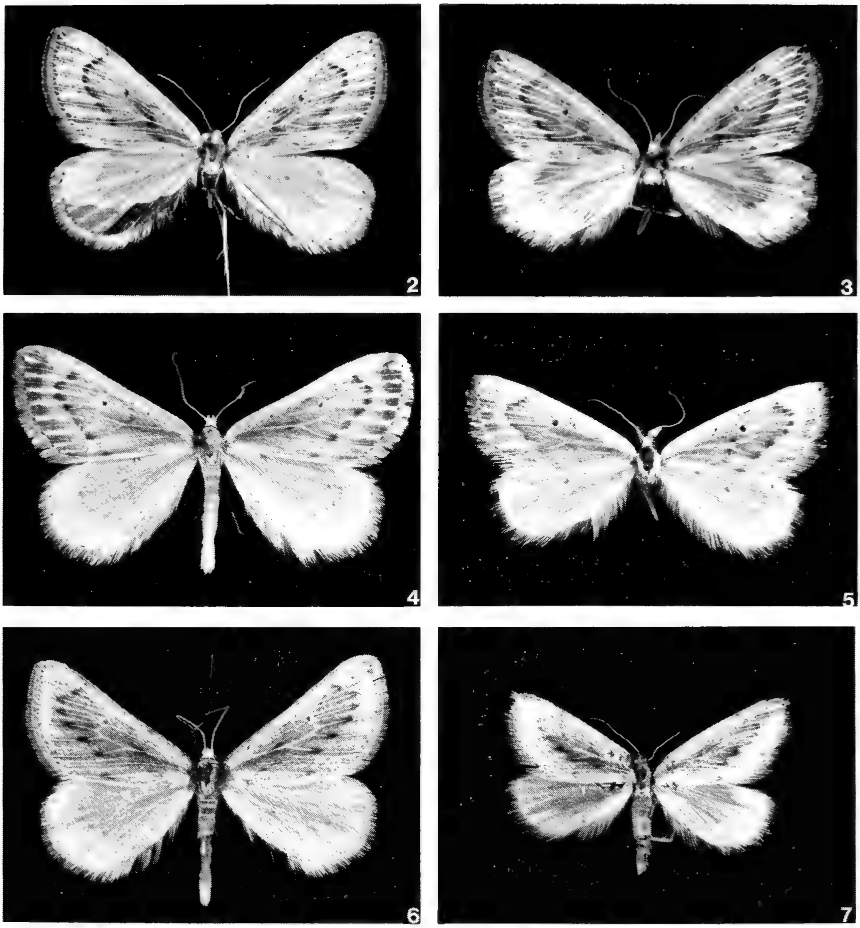
Sterrha interpunctaria : Herrich-Schäffer, 1840 : 104.
Eusarca interpunctaria : Herrich-Schäffer, 1847 : 34.
Eusarca interpunctaria : Herrich-Schäffer, 1848 : pl. 64, fig. 390.
Fidonia interpunctaria : Heydenreich, 1851 : 54.
Phasiane? *interpunctaria* : Lederer, 1853 : 180.
Selidosema? *interpunctaria* : Guenée, 1857 : 146.
Anisopteryx interpunctaria : Gumppenberg, 1893 : 396.
Eusarca interpunctaria : Staudinger & Rebel, 1901 : 322.
Eusarca interpunctaria : Spuler, 1904 : 86.
Eusarca interpunctaria : Spuler, 1907 : pl. 71b, fig. 1.
Myinodes interpunctaria : Prout, 1910 : 20, pl. 1, fig. 13.
Myinodes interpunctaria : Prout, 1912a : 4, pl. 1b.
Myinodes interpunctaria : Prout, 1912b : 32.
Eusarca interpunctaria : Culot, 1920 : 49, pl. 45, fig. 932.
Eusarca interpunctaria : Oberthür, 1922 : 307.
?*Myinodes interpunctaria* : Turati, 1925 : 8.
?*Myinos interpunctaria* : Krüger, 1939 : 352.
Myinoides interpunctaria : Mariani, 1943 : 81.
Myrinodes interpunctaria : Schmidlin, 1964 : 82.
Myrinodes interpunctaria : Parenzan, 1976 : 162, fig. 6a.
Myinodes interpunctaria : Fletcher, 1979 : 133.

MATERIAL EXAMINED : 1 ♂, Sicily, coll. Failla ; 1 ♂, S. Italy, Basilicata, F. Basento, Trivigno Scalo, 28.III.1977, leg. P. Parenzan, coll. ZSM ; 2 ♂♂, S. Italy, Puglia, Mte. Camplo, Laterza (TA), 21.III.1971, leg. P. Parenzan, coll. ZSM ; 16 ♂♂, Tunisia, Tunis distr., El Gouina, 9.II.-4.III.1960, leg. H.P. Müller, coll. ZSM ; 2 ♀♀, Algeria s., Algier Distr., El Aziza, 26.III.1989, leg. Kuchler jr., coll. K. Kuchler ; 1 ♀, Algeria, Constantine, leg. Olivier, coll. ZFMK ; 1 ♀, Algeria, Guelt-es-Stel, 19.IV.1931, leg. Predota, coll. ZFMK. 7 ♂♂, 3 ♀♀ dissected.

DISTRIBUTION (Fig. 1) : Sicily, S. Italy (Basilicata and Puglia), N. Tunisia, N. Algeria. The local populations of Tripolitania and Cyrenaica have to be preliminarily regarded as belonging to the nominate subspecies.

EXTERNAL MORPHOLOGY : Palpi : length 1.25-1.35 mm, scales dark brown, only upperside white. Frons (Fig. 8) with two projections. Length of cilia of male antenna about 0.14 mm, somewhat exceeding thickness of shaft (0.12 mm).

WINGS : Forewing length, male : 14.0-15.2 mm ; female (Algeria) : 11.4-13.7. Postmedial line very slightly dentate, at inner margin not inclined toward wing base. White intervenal line in subterminal area of forewing apex crossing postmedial fascia. Postmedial line and intervenal lines sharply bordered. Small terminal spots black, trianguliform, surrounded by forked white intervenal line.



Figs 2-7. *Myinodes* spp. 2 — *M. interpunctaria atlantica* ssp. n., ♂, Holotypus ; 3 — *M. interpunctaria atlantica* ssp. n., ♀, Paratypus ; 4 — *Myinodes constantina* sp. n., ♂, Holotypus ; 5 — *M. constantina* sp. n., ♀, Paratypus ; 6 — *M. shohami* sp. n., ♂, Holotypus ; 7 — *M. shohami* sp. n., ♀, Paratypus.

MALE GENITALIA (Fig. 10a-d) : Uncus short, with stout subapical processus. In juxta caudal median notch very deep, basis of juxta forked. Valva costa broad, smoothly edged. Caudal directed spine (harpe) prominent, pointed, slightly curved. Basal lobe of harpe strongly convex, with numerous small spines. Aedoeagus slender and long (mean 1.7 mm). Cornutus weakly sclerotised, situated subterminally. Aedoeagus bearing a longitudinal row of about four sharp, stoutly sclerotized teeth in terminal part. In the male from Sicily there are six teeth, perhaps an individual aberration. In the Tunisian males these teeth are isolated from each other.

Female genitalia (Fig. 14) : Females examined from Algeria have a comparatively long and narrow ductus bursae, its left lateral margin concave. Bursa copulatrix broad and large, but narrower than in the spanish subspecies. Caudal edge of lamella postvaginalis convex.

Habitat : Not above 900 m, mostly from 0-300 m. In Southern Italy abundant in a xerothermic locality (Mte. Camplo) with remnants of mediterranean macchia.

Flight period : Beginning of February to mid-April. The Tripolitanian specimen mentioned in Krüger (*l.c.*) taken in January.

Myinodes interpunctaria atlantica **subsp. n.** (Figs 2, 3)

Myinodes interpunctaria : Exposito, 1978 : 38.
Myiniodes interpunctaria : Rungs, 1981 : 223.

Holotype : ♂, S. Spain, Prov. S. Nevada, Alcolea, 5.IV.1991, leg. Kuchler jr., coll. ZSM, Prep.No. G 6825.

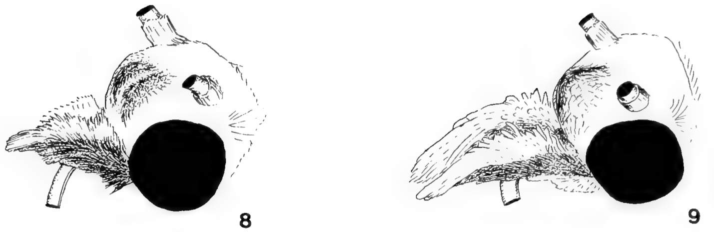
Paratypes : 1 ♀, S. Spain, Prov. S. Nevada, Alcolea, 1.IV.1991, leg. Kuchler jr., coll. ZSM ; 1♂, id., 5.IV.1991, leg. Kuchler jr., coll. K. Kuchler ; 1 ♂, S. Spain, Fuerte Higuera, Alicante, 2.IV.1993, leg. Kuchler jr., coll. K. Kuchler ; 3 ♂♂, S. Spain, Prov. Gador, Beria, 4.IV.1991, leg. Kuchler jr., coll. K. Kuchler ; 1 ♂, S. Spain, Prov. Cadiz, Villaluenga, 870m, 13.IV.1986, leg. et coll. A. Exposito ; 1 ♂, S. Spain, Prov. Malaga, Ronda, Cmo. Carbonera, 15.-28.III.1972, leg. et coll. A. Exposito ; 1 ♂, C. Spain, Toledo, 24.V.1972, leg. J. Calle, coll. A. Exposito ; 3 ♂♂, SW. Morocco, Marrakesch, O. Tensift, 12.III.1974, leg. Friedel, coll. M. Sommerer ; 1 ♂, id., coll. ZSM ; 1 ♀, W. Morocco, Zehroun, Mrassine, 1.-15.III.1921, leg. H. Powell, coll. ZFMK. 7 ♂♂, 3 ♀♀ dissected.

Distribution (Fig. 1) : C. and S. Spain, W. and N. Morocco.

External morphology : Palpi : Length in both sexes somewhat variable 1.00-1.25 mm, shorter than in nominate subspecies, dark brown, only upperside white. Frons with two projections. Length of cilia of male antenna about 0.11 mm, not exceeding thickness of shaft (0.11 mm).

Wings : Indistinguishable from *M. i. interpunctaria.* Forewing length, male : 13.6-16.8 mm ; female : 13.2-13.8 mm.

Male genitalia (Fig. 11a-d) : Uncus, juxta and costal part of the valva similar to *M. i. interpunctaria.* Harpe prominent, pointed, somewhat more curved than in nominate subspecies. Basal lobe of harpe slightly convex, not so heavily rounded. Aedoeagus slender and long



Figs 8, 9. Head of *Myinodes* spp. 8 — *M. interpunctaria* H.-S. ; 9 — *M. constantina* sp. n.

(mean 1.7 mm). Cornutus as in typical *M. i. interpunctaria.* Aedoeagus terminally heavily sclerotized, more than in nominate subspecies, bearing row of 3 or 4 sharp, lateral teeth.

FEMALE GENITALIA (Fig. 15) : Ductus bursae shorter and broader than in specimens from Algeria. Caudal edge of lamella postvaginalis slightly concave. Bursa copulatrix very similar, somewhat broader.

FLIGHT PERIOD : S. Spain mid-March to mid-April ; Morocco first half of March. The very late record from Toledo could indicate a later flight period in C. Spain, but this needs confirmation.

***Myinodes constantina* sp. n.** (Figs 4,5)

HOLOTYPE : ♂, Algeria, Lambèse, II-III.1913, leg. Sari Lakhdar ben Laouès, coll. ZFMK, Prep. No. Hausm. 7910.

PARATYPES : 4 ♂♂, Algeria, Lambèse, II-III.1913, leg. Sari Lakhdar ben Laouès, coll. ZFMK ; 1 ♂, id., coll. ZSM ; 1 ♀, Algeria, Guelt-es-Stel near Boghari, III-IV.1914, leg. Domenech Joseph, coll. ZSM ; 1 ♀, id., coll. ZFMK ; 1 , Tunisia, Kroumirie, Soudia, 24.V.1941, leg. Chnéour, coll. ZSM. 3 ♂♂, 2 ♀♀ dissected.

DISTRIBUTION (Fig. 1) : N. Algeria : Saharan Atlas and Constantine district. In Guelt-es-Stel sympatric with *M. interpunctaria.* NW. Tunisia.

EXTERNAL MORPHOLOGY : Palpi : Length in both sexes 1.40-1.60 mm, longer than in the other species, dark brown, upperside and basal scales near tongue white. Frons (Fig. 9) with only one central projection. Length of cilia of male antenna about 0.18 mm, exceeding thickness of shaft (0.12 mm).

WINGS : Forewing length, male : 14.7-15.7 mm ; female : 12.9-13.5 mm. Postmedial line not dentate, at inner margin strongly inclined toward wing base. White intervenal line in forewing apex very short, length about 1/3 of subterminal area. Postmedial line and intervenal lines indistinctly bordered. Antemedial line completely lacking. Small terminal spots black, punctiform. Intervenal lines near margin not forked, and not encircling terminal spots. Hindwings brighter than in the other species.

MALE GENITALIA (Fig. 12a-d) : Uncus long, with very small subapical processus. Caudal median notch of juxta very deep, caudal lobi pointed, basis convex. Costal part of valva sinus shaped. Harpe prominent, less pointed than in *M. interpunctaria*, strongly curved, without spines. Basal lobe of harpe lacking. Aedoeagus slender and very long (mean 1.9 mm). Cornutus situated subterminally, broader and more sclerotized than in *M. interpunctaria*. Aedoeagus terminally bearing a long digitiform and heavily sclerotized processus without teeth.

FEMALE GENITALIA (Fig. 16) : Ductus bursae long, straight. Bursa copulatrix small, irregularily shaped and not longitudinally ribbed as in the other species.

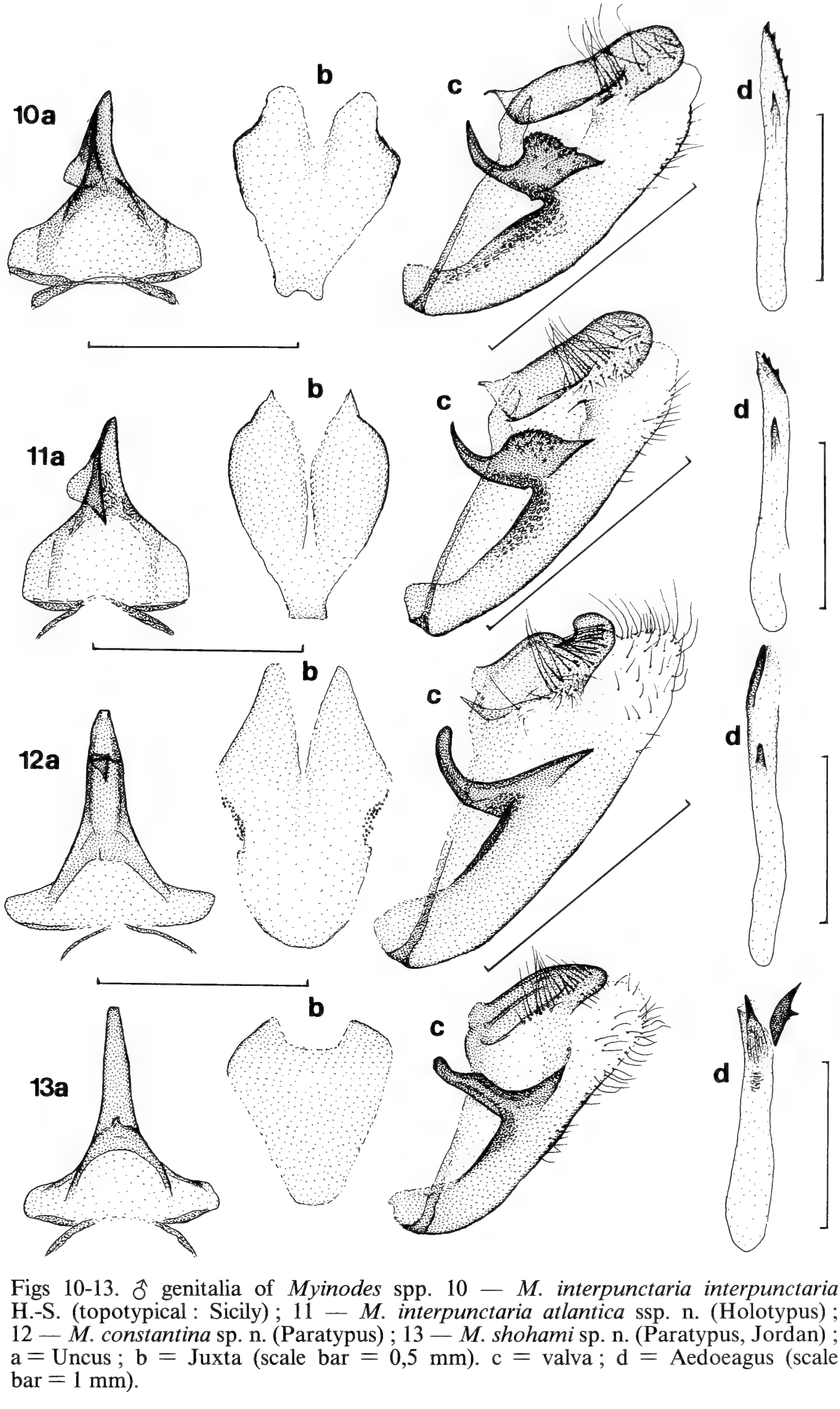
FLIGHT PERIOD : No precise data available (February to May?).

Myinodes shohami **sp. n.** (Figs 6, 7)

Pseudotagma interpunctaria : Staudinger, 1892 : 168.
Pseudotagma interpunctaria : v. Kalchberg, 1897 : 182.
Eusarca interpunctaria : Amsel, 1933 : 109.
Myinodes interpunctaria : Wehrli, 1934 : 2.
Eusarca interpunctaria : Bodenheimer, 1937 : 88.
Myinodes interpunctaria : Ellison & Wiltshire, 1939 : 43
Myinodes interpunctaria : Wiltshire, 1957 : 101.
Myinodes interpunctaria : Hausmann, 1991 : 115, pl. 10, fig. 63.

HOLOTYPE : ♂, NE. Jordan, Qasr el Hallabad, 17.II.1958, leg. Klapperich, coll. ZSM

PARATYPES : 1 ♂♀; C. Israel, En Gedi (Dead Sea), January, leg. G. Müller, coll. ZSM ; 1 ♂, id., III.1989 ; 1 ♀, id., 8.III.1989 ; 1 ♂, id., coll. TAU ; 1 ♂, C Israel, Enot Zuqim (Dead Sea), leg. G. Müller, coll. ZSM ; 3 ♂♂ 1 ♀, N. Israel, N. Ammud, 8.III.-19.III.1991, leg. R. Ortal, coll. ZSM ; 5 ♂♂, id., coll. TAU ; 1 ♂, N. Israel, Hula Reserve, 19.III.1991, leg. R. Ortal, coll. ZSM ; 2 ♂♂, id., 5.-8.III.1992 ; 1 ♂, N. Jordan, Amman, 8.II.1958 ; leg. Klapperich, coll. NLK ; 1 ♀, id., 28.VIII.1967 (date probably mislabelled) ; 1 ♂ 1 ♀, N. Jordan, Rumman, 28.II.1968, leg. Klapperich, coll. NLK ; 1 ♀, id., 28.II.1965, leg. Klapperich, coll. ZSM ; 3 ♂♂, N. Israel, Sede Nehamya, leg. Shoham, coll. BUS ; 1 ♂, id., coll. S. Yathom ; 1 ♂, N. Israel, Neot Mordehai, leg. Shoham, coll. BUS ; 1 ♂, N. Israel, Gazith, coll. TAU ; 1 ♂, C. Israel, "Palaestina", Tel Aviv, leg. Bodenheimer, coll. NHMW ; 1 ♀, N. Israel, "Syria", Haifa, coll. NHMW. 8 ♂♂, 3 ♀♀ dissected.



Figs 10-13. ♂ genitalia of *Myinodes* spp. 10 — *M. interpunctaria interpunctaria* H.-S. (topotypical : Sicily) ; 11 — *M. interpunctaria atlantica* ssp. n. (Holotypus) ; 12 — *M. constantina* sp. n. (Paratypus) ; 13 — *M. shohami* sp. n. (Paratypus, Jordan) ; a = Uncus ; b = Juxta (scale bar = 0,5 mm). c = valva ; d = Aedoeagus (scale bar = 1 mm).

FURTHER MATERIAL EXAMINED : About 20 more or less damaged specimens from N. and C. Israel, coll. ZSM ; 1 ♂, “Syria”, coll. NHMW ; 1 ♂, id., coll. ZSH ; 1 ♂, “Syria”, coll. ZFMK ; 4 ♂♂, S. Turkey, Taurus, Marasch, 600-900m, III.1930, leg. Einh. Slr., coll. ZFMK ; 1 ♂, id., coll. ZSH ; 1 ♂, S. Turkey, Amanus, “Syria”, Akbès, 1895, coll. ZFMK.

DISTRIBUTION : C. and N. Israel (AMSEL, 1933), N. Jordan (HAUSMANN, 1991), Lebanon (ELLISON & WILTSHIRE, 1939 : Beirut), S. Turkey (Marasch, Akbès, Mardin ; cf. WEHRLI, 1934) and N. Iraq (WILTSHIRE, 1957). As yet no species of this genus have been found in Egypt.

EXTERNAL MORPHOLOGY : Palpi : Length in both sexes 1.15-1.30 mm, much shorter than in *Myinodes constantina*, dark brown, upperside and basal scales near tongue white. Frons (cf. Fig. 9) with only one central projection. Length of cilia of male antenna about 0.16 mm, exceeding thickness of shaft (0.12 mm).

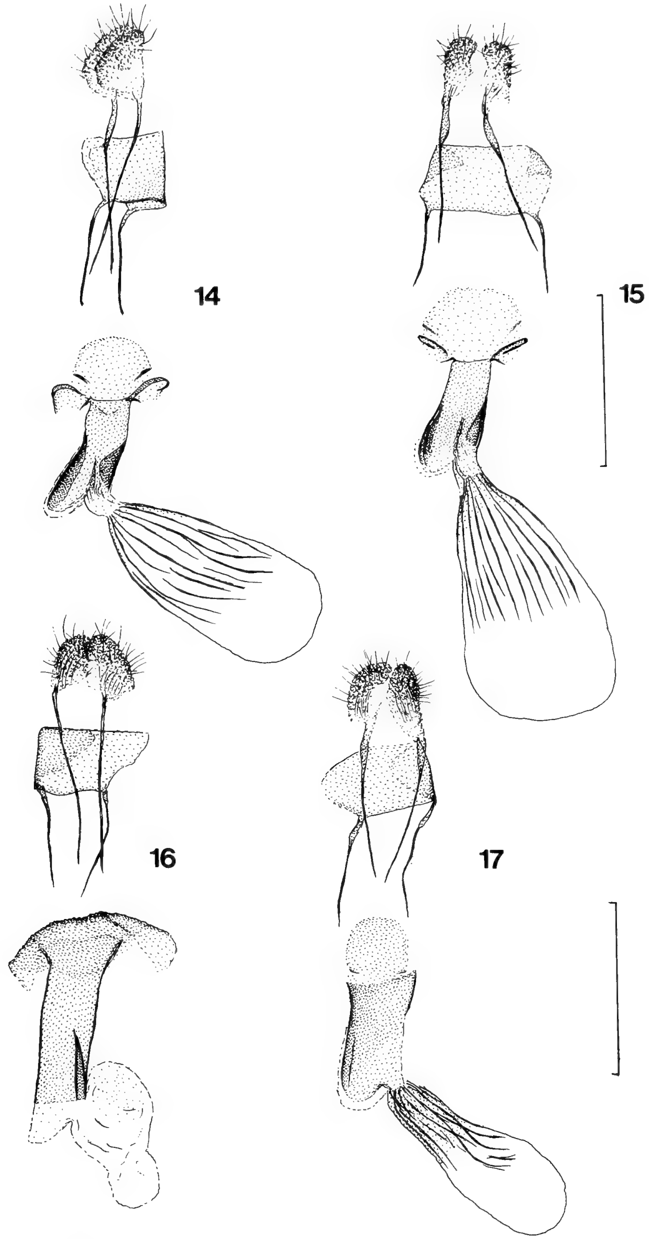
WINGS : Forewing length, male : 12.5-14.6 mm ; female : 10.6-11.4 mm. Postmedial line strongly dentate, more outwardly curved than in the other species, at inner margin not inclined toward base. White intervenal line in forewing apex longer than in *Myinodes constantina*, but not crossing postmedial fascia. Postmedial line and intervenal lines sharply bordered. Terminal spots black, punctiform and small, thinly encircled by white forked intervenal line. Forewings of specimens from S. Turkey slightly darker than in those from Jordan and Israel.

MALE GENITALIA (Fig. 13a-d) : Uncus very long, subapical processus lacking. Caudal excavation of juxta U-shaped, much less deep than in the other species, basis of juxta convex. Costal part of the valva narrower than in the other species, more convex and distally pointed. Harpe prominent, S-shaped, without spines. Basal lobe of harpe lacking. Aedoeagus comparatively broad and short (mean 1.55 mm). Cornutus terminally located, very stout. Aedoeagus apex laterally bearing heavily sclerotized, distally pointed plate with one or two lateral teeth.

FEMALE GENITALIA (Fig. 17) : Ductus bursae broad and short. Bursa copulatrix smaller and narrower than in *M. interpunctaria*. Caudal half of bursa copulatrix more sclerotized than in the other species.

HABITAT : From – 400 m (Israel) to 900 m (Taurus). In Israel and Jordan mainly in the swamps and wet areas near Hula Lake, the Dead Sea and some rivers (e.g. Zerqa, Nahal Ammud).

FLIGHT PERIOD : Israel and S. Turkey : Mid-February to end of March, one specimen in January (C. Israel). Jordan : Throughout February. One Jordan female labelled “28.VIII.” probably a mistake. In Iraq flying in April (WILTSHIRE, 1957).



Figs 14-17. ♀ genitalia of *Myinodes* spp. 14 — *M. interpunctaria interpunctaria* H.-S. (NE. Algeria) ; 15 — *M. interpunctaria atlantica* ssp. n. (Paratypus, S. Spain) ; 16 — *M. constantina* sp. n. (Paratypus) ; 17 — *M. shohami* sp. n. (Paratypus, N. Israel) ; scale bar = 1 mm.

REMARKS : Named after the late Mr. Z. Shoham, Israel, for his great merits in the lepidopterological exploration of N. Israel.

Key to species

1 Frons with two projections. Basal scales of palpi dark brown. Black terminal spots trianguliform. Intervenal line in forewing apex crossing postmedial line .... ***interpunctaria* H.-S.**
— Frons with only one central projection. Basal scales of palpi white. Black terminal spots punctiform. Intervenal line in forewing apex not crossing postmedial line **2**

2 Palpi long (ca. 1.5 mm). Postmedial line not dentate, at inner margin strongly inclined toward wing base. The white intervenal line in forewing apex very short .... ***constantina* sp. n.**
— Palpi short (ca. 1.2 mm). Postmedial line strongly dentate, at inner margin not inclined toward wing base. The white intervenal line in forewing apex approaching postmedial line .... ***shohami* sp. n.**

PARENZAN (1976 : fig. 9) mentions the genus *Myinodes* from N. and W. Turkey and Rumania, but gives no details. Confirmation of the occurrence of this genus from these areas is required.

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I wish to express my gratitude to Dr. D. Stüning, Bonn, P. Parenzan, Palermo, G. Ebert, Karlsruhe, A. Exposito, Mostoles, A. Freidberg, Tel Aviv, R. Ortal, Jerusalem, G. Müller, Jerusalem, K. Kuchler, Munich and M. Sommerer, Munich for the loan or donation of material.

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Nota lepid. 17 (1/2) : 44 ; 30.XI.1994 ISSN 0342-7536

Book reviews — Buchbesprechungen — Analyses

Larger moths of the London area. Colin W. Plant. xxii, 292 pp., 523 distribution maps 30.5 × 21.5 cm, hardback. London Natural History Society, 1993. ISBN 0 901009 04 0. Available from : The London Natural History Society, Publication sales secretary, 3 Chatsworth Gardens, West Harrow, Middlesex HA2 0RS, UK. Price : £ 19.95.

This volume can be considered to be the sequel to 'The butterflies of the London area' produced by the same author in 1987. It is however very different in both format and content. The moth volume has a much larger format, there are no coloured photographs and several species are treated per page. It will therefore not be attractive to the general public ; the 'moth hunter' however will find this book extremely interesting and useful.

The London area is defined as that area within 20 miles from St. Paul's Cathedral. All available records have been collated, but on the distribution maps, only the data obtained between 1980 and 1991 are plotted, although the older records are given in the usual way (open circles) for the rarer species. A transparent overlay with maps showing the built-up areas, woodland and chalk is provided. Over this ten year period, 84% of the 856 tetrads (a tetrad = 2 × 2 km) have been covered, although to varying degrees — a remarkable achievement. A total of 715 macrolepidoptera have been recorded from this area, although 66 were not noted during the ten year recording period. The text for each species is very readable, and reminiscent of that in South's 'Moths of the British Isles'. Foodplants known to have been recorded within the area are listed for each species, and also the years of the oldest and most recent records. Appendices give a check list of species for each vice-county in the area, the National Red Data List category, and the number and percentage of tetrads in which each resident species was recorded.

This work will undoubtedly be a very valuable tool for London naturalists, conservation officers and lepidopterists. It provides an ideal basis for further studies and the author and record contributors are to be congratulated on their efforts. Their example should be followed.

S. Whitebread

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Geographical variation in wing pattern of *Micropterix maschukella* Alphéraky, 1876 (Lepidoptera : Micropterigidae)

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Summary

Five discrete types of forewing pattern can be found within populations of *Micropterix maschukella* Alphéraky. In Lagodekhi, Eastern Georgia, frequencies of wing pattern types were the same for males and females ; no differences were found between the two study years. The frequency of wing pattern type was therefore considered to be a population specific character and was used to study geographical variation. Phenetic resemblances of 15 samples from the Crimea and Caucasus correspond in general to the spatial proximities of the sampling sites. Three geographically consistent units were distinguished : northern (Crimea and Krasnodar district), south-western and eastern. A clear allopatric differentiation within the species was found, but there was no corresponding variation in the male genitalia.

Résumé

Parmi les populations de *Micropterix maschukella* Alphéraky, on trouve cinq types discrets de dessin des ailes antérieures. A Lagodekhi, Georgie orientale, la fréquence des types de dessins des ailes est la même pour les mâles et les femelles ; on n'a pas trouvé de différences entre les deux années de l'étude. La fréquence des types de dessin des ailes a donc été considérée comme caractéristique des populations et utilisée pour étudier la variation géographique. Les ressemblances phénétiques de 15 échantillons de Crimée et du Caucase correspondent en général aux proximités spatiales des sites des échantillons. Trois unités géographiques consistantes ont été distinguées : nord (Crimée et région de Krasnodar), sud-ouest et est. On a constaté une nette différenciation allopatrique dans cette espèce, mais pas de variation correspondante dans les genitalia mâles.

Zusammenfassung

In Populationen von *Micropterix maschukella* Alphéraky lassen sich fünf Typen der Vorderflügelzeichnung unterscheiden. In Lagodekhi, Ost-Georgien, werden diese Zeichnungsmuster-Typen bei Männchen und Weibchen mit gleicher relativer Häufigkeit beobachtet ; zwischen den beiden Untersuchungsjahren gab es hierbei keine Unterschiede. Die relativen Häufigkeiten der Zeichnungsmuster-Typen wurden daher als populationsspezifisch betrachtet und als Maß für geographische Variabilität verwendet. Das Erscheinungsbild von 15 Sammelproben von der Krim und aus dem Kaukasus läßt sich im allgemeinem mit den räumlichen Abstand der Fundpunkte in Beziehung setzen. Drei geographische Bereiche lassen sich unterscheiden : ein nördlicher (die Krim und die Gegend von Krasnodar), ein südwestlicher und ein östlicher. Innerhalb der Art wurde eine deutliche allopatrische Differenzierung festgestellt, die aber nicht mit einer entsprechenden Variation der männlichen Genitalien verbunden ist.

Introduction

The contrasting wing pattern is typical for almost all of the approx. 70 species of the Palaearctic genus *Micropterix* Hübner [1825] (Heath, 1987). Wing pattern characteristics are widely used in determination keys (Razowski, 1975 ; Zagulajev, 1978 ; Kozlov, 1988 ; 1989 ; 1990a ; Whitebread, 1992), and they are of critical importance for the identification of females, whose genitalia are very poor in specific characters. However, variation of wing pattern characteristics has not been studied in this genus and the absence of knowledge of the extent of interpopulation and geographical variation has sometimes caused taxonomic problems.

The small (about 8-10 mm wing expanse) day-active irridescent moth *Micropterix maschukella* Alphéraky is widely distributed and very abundant in the Crimea and Caucasus. In Eastern Georgia the moths emerge at the beginning of May in the valleys ; at the altitudes 1500-1700 m the last specimens were observed in late July. The moths feed on the pollen of several plant species, usually on elder (*Sambucus nigra* L.) and *Philadelphus caucasicus* Koehne. Sometimes they also visit flowers of *Rubus* spp. and *Rosa* spp. (pers. obs.). The investigation of wing pattern variation has been prompted by the description of a new species, *Micropterix maritimella* (Zagulajev, 1983) based on females originating from the population of *M. maschukella* in Gantiadi, Abkhasia, which I had studied for some years.

Material and methods

The study consisted of two parts : intrapopulation variation was investigated in Lagodekhi Natural Reserve (Georgia, formerly the U.S.S.R. ; 41°50′ N, 46°20′ E) ; geographical variation was studied from specimens collected by the author and those kept in the Zoological Institute, St. Petersburg, Russia.

Moths were sampled from inflorescences of host plants by net and immediately anaesthetised by chloroform. Each sample was characterized by frequencies of moths with different wing pattern (see Figs 1-5) ; males and females were recorded separately. In total, about 5,500 moths were thus investigated. Samples were compared by chi-square test or, if the sample size was very small, by the non-parametric lambda criterion. Diversity (μ) was calculated according to Zhivotovsky (1982) :

$$\mu = (\Sigma_i \sqrt{p_i})^2,$$

where p_i is the frequency of the *i*th type of wing pattern ($i = 1...5$). The presence of geographical variation was tested by **G**-statistic for heterogeneity of proportions (Gabriel & Sokal, 1969). Pairwise similarity

$$\mathbf{R}_{k,l} = \Sigma_i \sqrt{p_{ik} p_{il}}$$

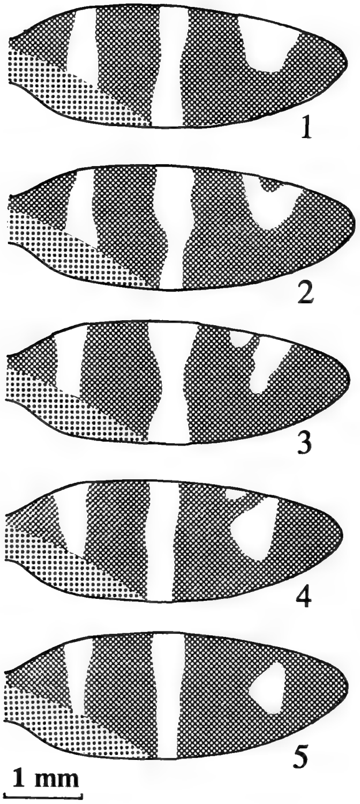
based on the ratio of frequencies (p_i) of all the wing pattern types (i) in populations under comparison (k and l) (Zhivotovsky, 1982) was calculated for all samples involved in the study ; similarity matrix was clustered on the base of mean arithmetic unweighed estimations of the similarity between clades.

Results

Wing pattern variation

The general appearance of the golden pattern in *M. maschukella* includes two bands (basal and medial) and a subapical spot, sharply distinguished from the cupreous-brownish background.

Five discrete types of forewing pattern were found. The first type has a large, almost rectangular subapical gold spot laying along the costal margin of the wing (Fig. 1). The second type differs from the first by having a small dark spot within this gold spot (Fig. 2). In both the third and fourth type there are two spots (small costal and large subapical) on the costal edge. These two types differ in the form of the subapical spot, which has its maximum width either at the costal margin (type 3, Fig. 3), or towards the centre of the wing (type 4, Fig. 4). The 5th type differs from the 4th due to the absence of the costal spot ; the large subapical spot is usually not connected to the costal edge of the wing (Fig. 5), although there are some exceptions.



Figs 1-5. The five types (numbers 1-5) of forewing pattern of *M. maschukella*.

The two bands, although variable in form and width, did not show any clearly recognizable types.

The right and left wings of the moth usually have the same type of wing pattern. However, 30.6% of specimens collected in Lagodekhi 1989 and 28.7% in 1990 were asymmetrical. But if the pattern of the right and left wing varies independently, the expected number of asymmetrical moths would be significantly (about 2 times) higher than observed (in 1989 : expected 64.0%, $G = 799.1$, $df = 1$, $P < 0.0001$; in 1990 : expected 56.9%, $G = 291.9$, $df = 1$, $P < 0.0001$). In spite of the high percentage of asymmetrical specimens, some genetic background of wing pattern types is assumed. But even if the variation is phenotypic only, it does not affect the conclusions of the present study.

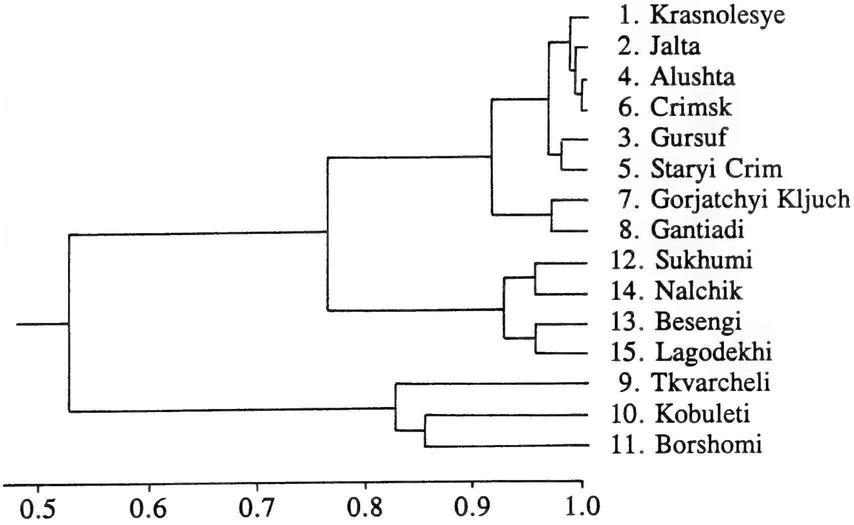


Fig. 6. Dendrogram based on the similarity between samples of *M. maschukella* in wing pattern frequency.

In spite of the very low (about 10%) proportion of males in samples obtained from the inflorescences of elder in Lagodekhi, I succeeded in obtaining samples of 15-25 males from six local populations ; differences between sexes appeared to be non-significant (lambda = 0.04-1.10). Differences between samples obtained in Lagodekhi in 1989 and 1990 from the same local populations were also not significant. Thus, I concluded that the frequencies of wing pattern types are relatively stable in time, and therefore the samples collected in different years can be compared when studying geographical variation. To increase the sample size, males and females were pooled when counting wing pattern frequencies.

Geographical variation

The 15 localities in the Crimea and Caucasus, significantly heterogeneous in wing pattern frequencies ($n = 5242$, $G = 1383.6$, $df = 52$, $P < 0.0001$), were included in the analysis. Clustering of the similarity matrix showed that the phenetic resemblances of samples correspond in general to their spatial proximities (Fig. 6). Three geographically consistent units were distinguished : northern (Crimea and Krasnodar district), south-western and eastern (Fig. 7).

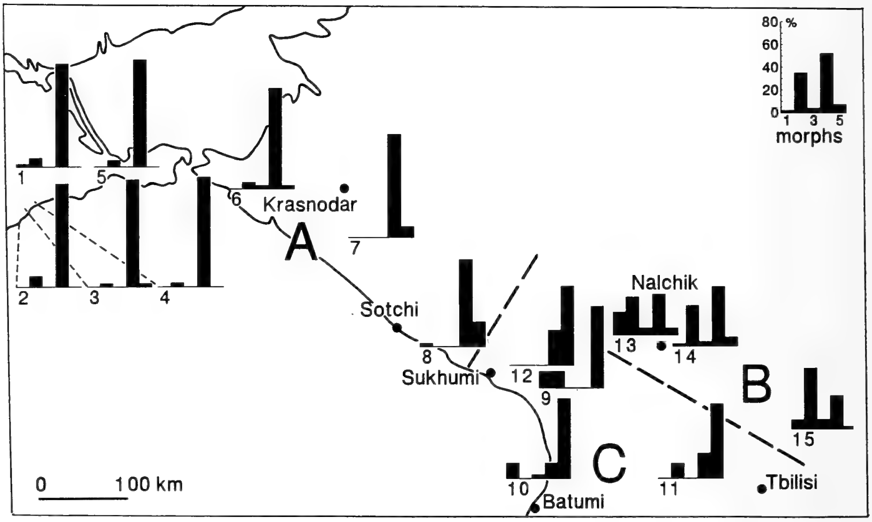


Fig. 7. Geographical variation in wing pattern frequencies of *M. maschukella* Alph. in the Crimea and Caucasus. Localities : 1 — Krasnolesye (sample size n = 94, moths collected in 1984) ; 2 — Jalta (n = 54, 1983) ; 3 — Gursuf (n = 60, 1985) ; 4 — Alushta (n = 72, 1983) ; 5 — Staryi Crim (n = 36, 1913) ; 6 — Crimsk (n = 36, 1990) ; 7 — Gorjatchyi Kljuch (n = 22, 1988) ; 8 — Gantiadi (n = 42, 1978) ; 9 — Tkvarcheli (n = 14, 1980) ; 10 — Kobuleti (n = 66, 1973) ; 11 — Borshomi (n = 46, 1898) ; 12 — Sukhumi (n = 26, 1980) ; 13 — Besengi (n = 70, 1989) ; 14 — Nalchik (n = 54, 1989) ; 15 — Lagodekhi (n = 4550, 1990). Contours correspond to the clusters identified in Fig. 6. Groups of population : A — northern ; B — eastern ; C — south-western.

Samples from the northern group demonstrated the lowest observed intrapopulation diversity (coefficient of diversity $\mu < 2.5$) ; about 90% of individuals belonged to the fourth type of wing pattern. This group was heterogeneous ($n = 416$, $G = 59.4$, $df = 28$, $P < 0.0005$) because of the most southern sample (from Gantiadi), which had an intermediate ratio of wing pattern types. If this sample is excluded from the consideration, the northern group becomes homogeneous in relation to wing pattern frequencies ($n = 374$, $G = 28.3$, $df = 24$, $P < 0.251$).

Both the south-western and eastern groups are significantly heterogeneous ($n = 126$, $G = 30.1$, $df = 8$, $P < 0.0005$, and $n = 4700$, $G = 168.2$, $df = 12$, $P < 0.0001$, respectively), and more diverse than the northern one ($\mu = 3.5$-4.5). In the south-western group the pattern number five was most abundant, in contrast to the eastern group where the second and fourth types had highest frequencies. The small number of localities being compared did not allow investigation of the geographical variation of wing pattern within these groups.

Discussion

Like leaf miners of the family Nepticulidae (Menken, 1990), *M. maschukella* bear characteristics which appear to facilitate rapid speciation : they occur in small isolated populations, the detritophagous caterpillars and pollen-eating adults have only a few (if any) competitors, and their food resources are highly predictable. But, in contrast to sympatric speciation in Nepticulidae and Yponomeutidae (Menken, 1990 ; Menken *et al.*, 1992), Micropterigidae demonstrate mostly geographical (allopatric) differentiation.

No differences in genitalic structure were found between males of *M. maschukella* with different wing patterns, or between local populations in Lagodekhi area and between populations from different geographical groups (Kozlov, 1990b and unpublished data). According to the recognition concept of species argued by Paterson (1985), this may be due to visual recognition of the opposite sex in this moth species. In this respect *M. maschukella* is similar to butterflies, which often demonstrate strict interspecific differentiation in wing pattern features, while male genitalia are quite similar, i.e. in the genus *Erebia* Dalm. (Warren, 1936).

Thus, the data obtained showed clear allopatric differentiation within the species, which, however, demonstrated no corresponding variation in male genitalia structure. It is possible that a complex of subspecies or even sibling species may exist under the name *Micropterix maschukella*, but at the present level of knowledge the differentiation in wing pattern is not sufficient to ascribe a taxonomic rank to geographically separated populations.

Acknowledgements

I am very grateful to V. Pavliashvili and all the staff of the Lagodekhi reserve for their hospitality during my stay in Georgia. I am greatly indebted to M. Motorkin for his assistance in collecting the moths, E. Zvereva for fruitful discussion, E. Haukioja, N. P. Kristensen, M. R. McClure and T. Vuorisalo for their helpful comments and improvement of the text. The work was supported by the Plant Protection Institute (St. Petersburg, Russia) and the University of Turku Foundation (Finland).

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Eine weitere endemische Hepialide aus den Alpen : *Pharmacis claudiae* sp. n. (Lepidoptera : Hepialidae)

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Summary

Another new endemic Hepialid from the Alps : *Pharmacis claudiae* sp. n. (Hepialidae) — A new species allied to *Ph. bertrandi* (Le Cerf) and *Ph. anselminae* (Teobaldelli) is described from the Italian Alps (Aosta, Valtournenche) based on a series of males. It differs from the related taxa in wing markings, genital morphology and male activity period. The probably brachypterous female is still unknown.

Résumé

Une espèce nouvelle proche de *Ph. bertrandi* (Le Cerf) et de *Ph. anselminae* (Teobaldelli), est décrite des Alpes italiennes (Aoste, Valtournanche), fondée sur une série de mâles. L'espèce se distingue des taxa voisins aussi bien par l'habitus que par les genitalia. En plus, elle diffère de *Ph. anselminae* et de *Ph. carna* (Denis & Schiffermüller) par la phase d'activité du mâle. La femelle, probablement brachyptère, reste encore inconnue.

Zusammenfassung

Pharmacis claudiae sp. n. wird aus den italienischen Alpen (Aosta, Valtournenche) anhand einer Serie von männlichen Faltern beschrieben. Die Art unterscheidet sich sowohl habituell als auch genitalmorphologisch von den verwandten Taxa *Ph. bertrandi* (Le Cerf) und *Ph. anselminae* (Teobaldelli). Zu *Ph. anselminae* und *Ph. carna* (Denis & Schiffermüller) bestehen zudem Unterschiede in der Aktivitätsphase der Männchen. Das vermutlich brachyptere Weibchen ist noch unbekannt.

Einleitung

Die Entdeckung einer bisher unbekannten Lepidopteren-Spezies in Mitteleuropa ist in heutiger Zeit ein seltenes Ereignis. Nach selbstkritischer Beurteilung der vorliegenden Fakten, dem Vergleich von Serien von Genitalpräparaten und nach Einbeziehung genealogischer Überlegungen halten die Verfasser die Aufstellung eines neuen Taxons im Artrang für gerechtfertigt. Es ist wohl daher auch vertretbar, über die nüchterne wissenschaftliche Dokumentation hinaus eine kurze Beschreibung der Entdeckung des neuen Taxons beizufügen.

Die Entdeckungsgeschichte von *Pharmacis claudiae*

(P. M. Kristal)

Am 28. Juli 1992 unternahmen wir (Claudia Kuon, Norbert Hirneisen und Philipp M. Kristal) während unseres Aufenthalts im Aosta-Tal (Italien) eine Tagestour zum Monte Cervinio (Matterhorn) am Ende des Valtournenche. Von der Talstation in Breuil-Cervinia fuhren wir mit der Seilbahn zum Giomein, also zur ersten Station auf ca. 2100 m Höhe. Von dort streiften wir durch das Gelände und fanden neben vielen hochalpinen Tagfalterarten auch einen Wurzelbohrer. Nach anstrengender Jagd auf den in unruhigem Zickzackflug über die alpinen Matten fliegenden Falter wurde diese *Pharmacis* "*carna*" von Norbert Hirneisen zur Präparation und Artbestimmung an Philipp Kristal übergeben, der diese "etwas dunkle *fusconebulosa*" gerne übernahm, da ihm weder die eine noch die andere Art aus seinen 12 Aufenthalten im Aosta-Tal bekannt war.

Nach unserem Abstieg stand für uns fest, daß wir am Abend in der Nähe, "irgendwo über 2000 m" Lichtfang betreiben wollten. Da Philipp Kristal durch seine jahrelange Tätigkeit für das naturwissenschaftliche Museum in St. Pierre, Aosta-Tal, eine Genehmigung zum Befahren gesperrter Wege im gesamten Tal besaß, war nur das Problem des Anfahrens eines Leuchtplatzes gegeben. Erfahrungsgemäß erweisen sich auf der Karte verzeichnete Wege oftmals als nur für allradgetriebene Fahrzeuge befahrbar, so daß wir erst nach mehreren Fehlversuchen schließlich einen schönen Platz oberhalb von Antey-Saint-André bei Telinaud auf ca. 2200 m Höhe fanden.

Das Terrain dort war spärlich bewachsen und auf den wenigen üppiger bewachsenen Matten grasten die Rinder der nahen Alpe. Nur noch einzelne Lärchen und Föhren umgaben uns, wir befanden uns dort offensichtlich direkt an der Waldgrenze. Dieser Platz erinnerte mich sehr stark an die mir bekannten Fundorte von *Pharmacis anselminae* im Val di Valeille und im Champorcher-Tal, da auch dort eine relativ starke Beweidung der *Ph. anselminae*-Biotope stattfindet. Diese Beweidung scheint den Wurzelbohrern offensichtlich nicht zu schaden, wahrscheinlich ist dieser Umstand für die *Ph. anselminae*-Populationen sogar förderlich, wenn nicht sogar überlebenswichtig.

Nachdem uns Claudia Kuon trotz größter Schnakenplage ein Abendessen in der "Feldküche" gezaubert hatte, konnten wir gut gestärkt mit dem Aufschlagen unserer beiden Leuchttürme beginnen, die wir mit einer Distanz von ca. 150 m errichteten. Der Anflug war, durch einen vom Tal aufsteigenden Wind begünstigt, sehr gut und wir hatten alle Hände voll zu tun, um alle anfliegenden Arten qualitativ und — soweit möglich — auch quantitativ zu erfasen. Gegen 1 Uhr Sommerzeit begab sich jeder noch einmal zu seinem Turm, um nach einem letztmaligen Absuchen des Leuchtplatzes mit dem Abbau zu beginnen. Uns fielen sofort die erst jetzt in Anzahl anfliegenden Wurzelbohrer auf, die wegen ihrer Größe, der sehr dunklen, fast schwarzen Grundfarbe und der grellweißen Zeichnung nicht sofort einer uns bekannten Art zuzuordnen waren. Durch die Distanz zwischen unseren Leuchttürmen konnten wir uns nicht sofort verständigen, und erst vor der Abfahrt konnten wir uns über diesen Bohrer unterhalten. Da Norbert Hirneisen nur ein Belegtier mitgenommen hatte, erwies es sich als vorteilhaft, daß Philipp Kristal im Hinblick auf die Lokalsammlung des Museums in St. Pierre zwölf Tiere im Fangglas hatte, so daß genügend Anschauungsmaterial vorhanden war.

Wir saßen in dieser Nacht noch lange über dieser Hepialide, die nach den Abbildungen bei FORSTER & WOHLFAHRT (1960) keiner uns bekannten Art zuzuordnen war. Überdies fiel uns auf, daß nach den Angaben dort *Pharmacis carna* und *Ph. fusconebulosa* ebenfalls ausscheiden müßten, da *carna* erst gegen Morgen zum Licht kommt, *fusconebulosa* jedoch in der späten Abenddämmerung fliegt. Aus eigener Erfahrung wußten wir, daß *anselminae* tagaktiv ist. "Unser" Bohrer jedoch kam ziemlich genau kurz nach 24 Uhr MEZ zum Licht. Da die Zeit des Paarungsflugs in der Regel genetisch festgelegt ist, kamen wir überein, daß wir uns diesen Bohrer doch noch näher ansehen müßten, denn es sei nicht auszuschließen, daß wir eine weitere, im Aosta-Tal endemische Art vor uns hätten, nachdem der Endemit *Pharmacis anselminae* auch erst vor ca. 15 Jahren von Teobaldelli im Aosta-Tal entdeckt worden war.

Wir opferten unsere restliche Urlaubszeit diesem Unterfangen und konnten in drei Nächten noch weitere 6 Tiere am Licht erbeuten. Die Nachsuche nach Puppen oder Weibchen bei Tage, wie bei *anselminae* schon erfolgreich praktiziert, blieb jedoch in diesem Falle ohne greifbares Ergebnis. Beim Anfertigen der Genitalpräparate stellte sich heraus, daß wir, wie vermutet, nur männliche Falter am Licht erbeutet hatten und daß das Tier von oberhalb Breuil di Cervinio zur gleichen Art gehörte wie die Tiere von Antey-Saint-André.

Pharmacis claudiae Kristal & Hirneisen sp. n.

Locus typicus : Italia, Aosta, Valtournenche oberhalb Antey-Saint-André (1), 2200 m.

Holotypus ♂ : Italia, Aosta, Valtournenche oberhalb Antey-Saint-André, 2200 m, 31.7.1992, Lichtfang, leg. Kristal, coll. British Museum (Natural History) London.

Paratypen : 19 ♂♂ gleicher Fundort wie Holotypus, 28.7., 31.7. und 1.8.1992, leg. Kristal & Hirneisen. Coll. British Museum (Natural History) London (1), coll. Staatliches Museum für Naturkunde Karlsruhe (2), coll. Museum Witt, München (2), coll. Museo di Scienze Naturali, St. Pierre, Aosta (2), coll. Kristal (9), coll. Hirneisen (3) ; 1 ♂ Italia, Aosta, oberhalb Breuil di Cervinio, ca. 2000 m, 28.7.1992, Tagfang, leg. Hirneisen, coll. Kristal.

Habitus (Abb. 1-2) : Spannweite 38-42 mm, Ø 40,5 mm (n = 17). Vorderflügellänge 18-20,5 mm, Ø 19 mm (n = 17). Kopf und Thorax dunkelbraun. Vorderflügel dunkelbraun, im postmedianen Bereich mit zwei weißen, fast parallel verlaufenden Fleckenreihen, von denen die äußere nicht durch Wische mit dem Außenrand verbunden ist. Auch die übrige Flügelfläche ist mit mehr oder weniger deutlich ausgebildeten weißen Flecken überdeckt. Alle weißen Zeichnungselemente sind, wie bei *Ph. carna*, durch doppelte dunkle Linien begrenzt, die hellbraun ausgefüllt sind. Die bei *Ph. carna* in den Apex ziehende, kettenartig verbundene, hellbraun umsäumte, dunkle Fleckenreihe ist bei *Ph. claudiae* als dunkle, hellbraun begrenzte Binde ausgebildet, die ca. 3 mm vom Analwinkel entfernt entspringt und 2 bis 3 mm vor dem Apex auf die Costa trifft. Die Fransen der Vorderflügel sind deutlich hell und dunkelbraun gescheckt, ebenso die der Hinterflügel bis vor den Analwinkel.

Männlicher Genitalapparat (2) (Abb. 6-11) : Valven sehr lang und schmal, schwach gebogen. Vinculum auffallend durch die konvexe Ausbuchtung am ventralen Rand und die starke konkave U-förmige Einbuchtung zwischen den zwei stark sklerotisierten, triangulären Vinculumfortsätzen. Pseudoteguminalplatte (Mesosoma bei Nielsen &

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(1) Auf eine genauere Beschreibung der Fundlokalität wird hier mit Rücksicht auf den endemischen Charakter der Art und die damit verbundene Schutzproblematik verzichtet. Die Erfahrungen bei *Pharmacis anselminae* haben gezeigt, daß es leider genug verantwortungslose sogenannte "Entomologen" gibt, die sich nicht scheuen, an einem Tag an einer Flugstelle von einer nur sehr lokal vorkommenden Art mehrere Dutzend "Belegtiere" einzusammeln. Diesem Sammeltourismus soll kein Vorschub geleistet werden.

(2) Die (bei den Hepialiden noch immer uneinheitliche) Genitalterminologie richtet sich nach Nielsen & Kristensen (1989).

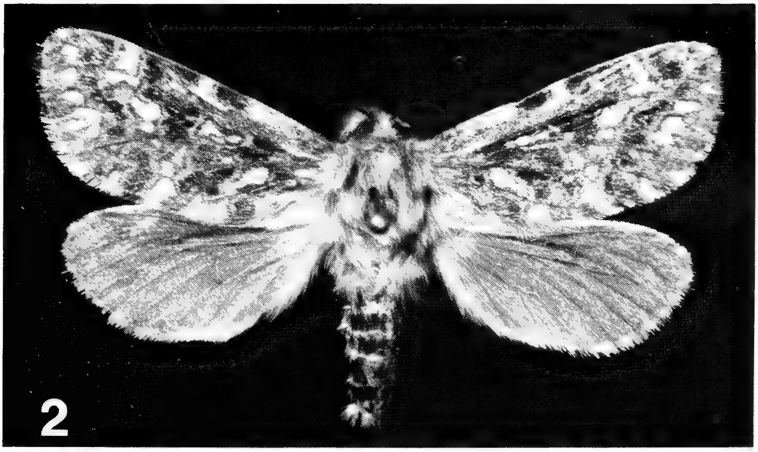

Abb. 1, 2. *Pharmacis claudiae* sp. n. ♂, Italien, Aosta, Valtournenche. 1 — Holotypus ; 2 — Paratypus.

Robinson, 1983) im oberen Teil breit, medial nicht verschmolzen, die oberen medialen Spitzen in der Form variabel, teils schmal, teils breiter, gelegentlich papageienschnabelartig geformt, aber immer einheitlich schwach sklerotisiert ; Pseudoteguminalarme verschmolzen und eine stark gefaltete Rinne bildend. Ventraler Rand der Juxta flach konkav gebogen.

Differentialdiagnose : Im Habitus von *Ph. anselminae* unterschieden durch die bedeutendere Größe (Spannweite 38-42 mm gegen-

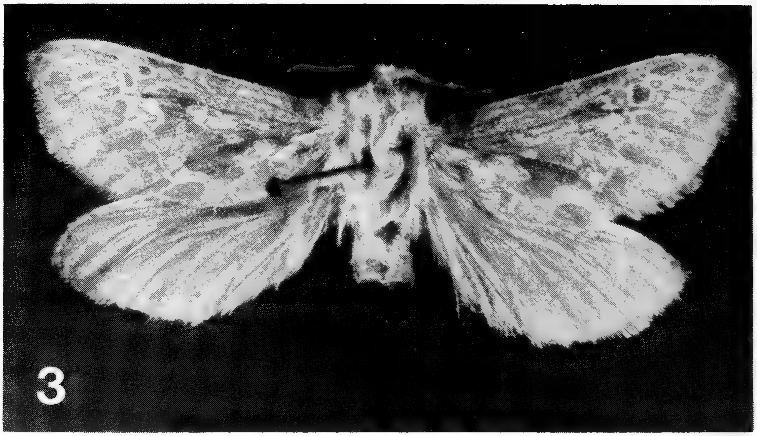

Abb. 3. *Pharmacis bertrandi* (Le Cerf) ♂. Frankreich, Hautes-Alpes, Chamonix.

über 28-33 mm bei *anselminae*), durch die weißlichen bis rein weißen, hellbraun umrandeten Fleckenzeichnungen (bei *anselminae* hellockerbraun und ohne irgendwelche Umrandung) und durch die auf beiden Flügeln deutlich hellbraun-dunkelbraun gescheckten Fransen (bei *anselminae* Hinterflügelfransen einfarbig, Vorderflügelfransen manchmal mit schwach angedeuteter Scheckung am Tornus). Von *Ph. bertrandi* im Habitus unterschieden durch die dunkelrotbraune bis schwärzlichbraune Grundfarbe (bei *bertrandi* hell- bis mittelbraun) sowie durch die gescheckten Fransen (bei *bertrandi* einfarbig). Im männlichen Genitalapparat unterscheidet sich *claudiae* von beiden Arten durch die sehr langen, schmalen Valven (bei *bertrandi* und *anselminae* wesentlich kürzer, nahezu erdnußförmig) und durch die U-förmige Einbuchtung zwischen den triangulären Vinvulumfortsätzen, von *bertrandi* außerdem durch das Fehlen der sternförmigen Sklerotisierung an der oberen medialen Spitze der Pseudoteguminalplatte und durch die unterschiedliche Form des ventralen Randes der Juxta. *Ph. claudiae* ist nachtaktiv, *Ph. anselminae* tagaktiv.

Weibchen : noch unbekannt. Die nahe Verwandtschaft zu den Arten mit brachypteren Weibchen, die (soweit bisher bekannt) stark eingeschränkte, endemische Verbreitung sowie die Tatsache, daß alle am Licht anfliegenden Tiere Männchen waren, deuten darauf hin, daß es sich auch bei *Ph. claudiae* um eine im weiblichen Geschlecht kurzflügelige Art handeln könnte.

Aktivitätsphase : Die Aktivitätsphase der Männchen fällt ziemlich genau auf die Zeit zwischen 0 und 1 h MEZ. Ein einzelnes, wohl auf-

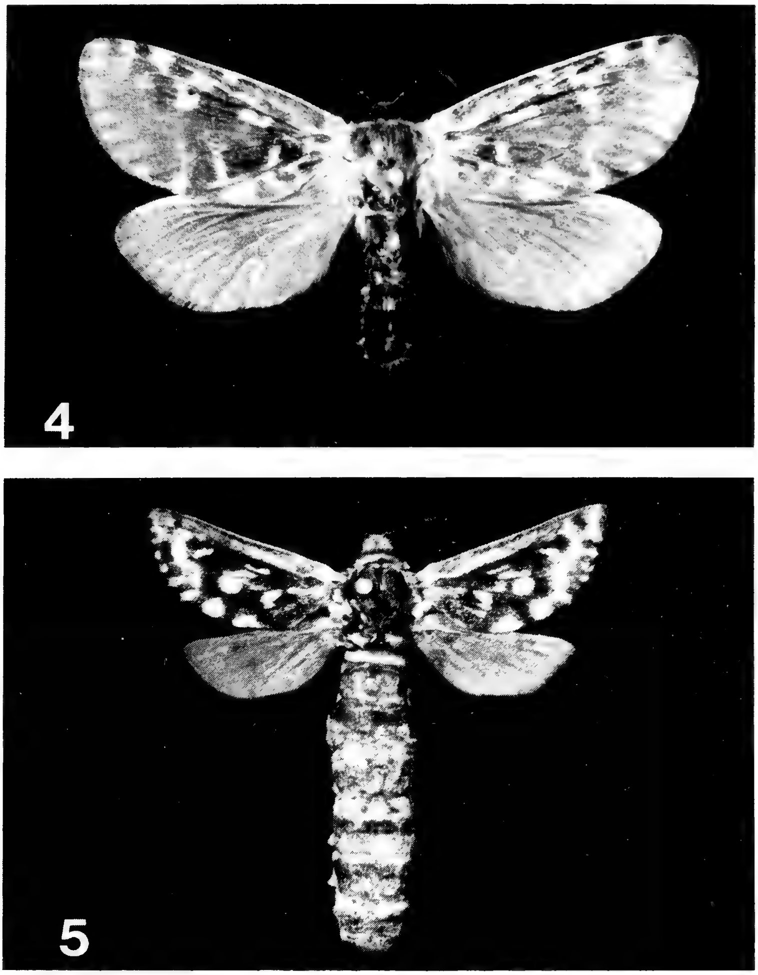

Abb. 4, 5. *Pharmacis anselminae* (Teobaldelli), Italien, Aosta, Val Cogne. 4 — ♂; 5 — ♀.

gescheuchtes Tier wurde am Nachmittag gegen 14.30 h MEZ in reißendem Flug über die alpinen Rasen fliegend gefangen. Dies dürfte einen Ausnahmefall darstellen, da am betreffenden Fundort trotz Aufmerksamkeit kein weiteres tagaktives Tier beobachtet wurde.

Verbreitung : Italienische Alpen, Aosta, Valtournenche zwischen Breuil-Cervinia an den Südhängen des Matterhorns und Antey-St.-André. Die bekannten Areale von *Ph. anselminae* und *Ph. claudiae*

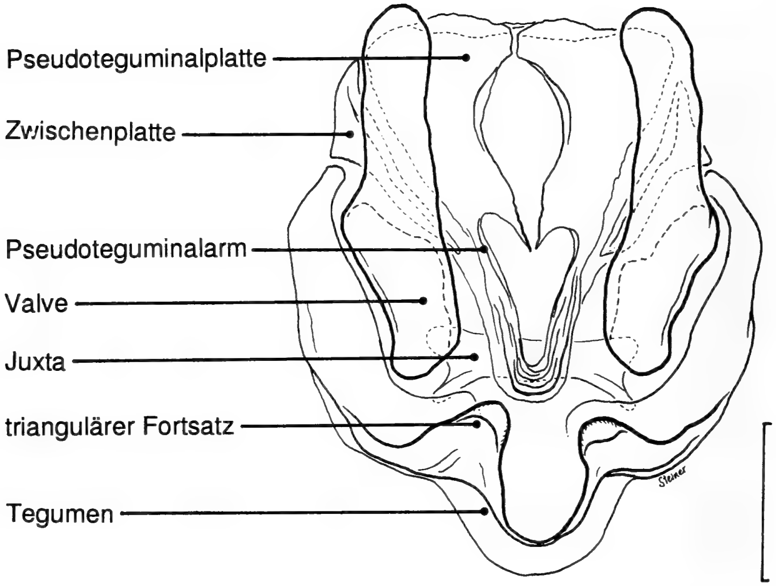

Abb. 6. *Pharmacis claudiae* sp. n. männliche Genitalien. Italien, Aosta, Valtournenche. Holotypus. Der dorsale Teil der Juxta proximal umgebogen. Maßstab 0,5 mm.

sind damit nur um ca. 25 km (Luftlinie) voneinander entfernt, aber durch das tief eingeschnittene Valle d'Aosta getrennt, das für Arten mit flugunfähigen Weibchen eine unüberwindbare Barriere darstellt. Beide Arten müssen das Würmglazial in unvergletscherten Refugien überdauert haben, *Ph. claudiae* nördlich des Aostatals und *Ph. anselminae* südlich davon.

VERTIKALVERBREITUNG : Die bisher bekannten Fundstellen liegen in Höhen zwischen 2000 und 2200 m.

BIOTOP : Alpine Rasen oberhalb der Waldgrenze (Abb. 23).

FLUGZEIT : Nachgewiesen vom 28. Juli bis zum 1. August. Es ist zu vermuten, daß *Ph. claudiae* eine ähnlich kurze Flugzeit hat, wie sie für *Ph. bertrandi* anhand der vorliegenden Daten zu vermuten ist und für *Ph. anselminae* beobachtet wurde. Eine kurze Flugzeit von einer Woche bei sehr lokaler Verbreitung erklärt sowohl die späte Entdeckung der Arten *Ph. claudiae* und *Ph. anselminae* als auch das spärlich vorhandene Material bei *Ph. bertrandi.* Es sollte an dieser Stelle auch die von DANIEL (1950) für *Ph. carna* aufgestellte Vermutung einer nur eintägigen Lebendauer der Männchen in die Überlegungen zur Biologie der Arten einfließen, obwohl gerade *Ph. carna* eine ausgedehnte Flugzeit hat.

Derivatio nominis : Die Namensgebung erfolgt zu Ehren unserer bezaubernden Kollegin, Frau Claudia Kuon, die uns in den kalten Hochgebirgsnächten immer begleitete, verpflegte und die erschöpften Entomologen im Morgengrauen sicher nach Hause fuhr. Sie war trotz des mehr als 60 km weiten Anfahrtsweges durchs Gebirge und der dort oben herrschenden Schnakenplage stets gut aufgelegt und half uns somit in nicht zu unterschätzender Weise.

Verwandte Arten

Pharmacis bertrandi (Le Cerf, 1936)

Untersuchtes Material : 1 ♂ mit 2 Etiketten : "*Hepialus Bertrandi* Le Cerf 20.VII.1954 [France,] Chamonix H[au]t[es] Alpes" und "coll. Th. Witt München/ Weiden Ht. Alpes Chamonix 20.VII.1954 leg. Rungs", coll. Museum Witt, München.

Habitus (Abb. 3) : Spannweite 37 mm (n = 1) ; Teobaldelli (1977) und Freina & Witt (1990) : 35-39 mm. Vorderflügellänge 17 mm (n = 1). Die Zeichnungselemente sind ähnlich wie bei *Ph. carna* angelegt. Die Grundfärbung ist etwas heller, die weißen Flecken sind weit spärlicher vorhanden. Zwei bis drei kleine Fleckchen bilden, deutlicher als bei den verwandten Arten, eine weiße Basalstrieme. Die kettenartige, aus hellbraun umrandeten runden Fleckchen bestehende Binde entspringt hier ebenfalls im Analwinkel des Vorderflügels, zieht gerade verlaufend zur Costa und trifft ca. 1 mm vor dem Apex auf die Costa. Die Fransen aller Flügel sind einfarbig dunkelbraun.

Männlicher Genitalapparat (Abb. 12) : Valven gebogen, kürzer als bei *Ph. claudiae*, in der Mitte etwas eingeschnürt, dadurch in der Form an eine Erdnuß erinnernd. Ventraler Rand des Vinculum regelmäßiger gerundet als bei *Ph. claudiae* und *Ph. anselminae*. Einbuchtung zwischen den triangulären Vinculumfortsätzen grob U-förmig bzw. (am ventralen Rand der stark sklerotisierten Zone) abgerundet W-förmig (vgl. auch Teobaldelli, 1977, Abb. 3).

Weibchen : Die Weibchen sind brachypter.

Aktivitätsphase : Den Verfassern sind keine Angaben bekannt.

Verbreitung : Französische Alpen, Alpes-Maritimes (Guil-Tal) und Hautes-Alpes (Abriés). Das vorliegende Belegstück ist mit "Chamonix" bezettelt, wobei nicht eindeutig klar ist, ob es sich, wie auf dem Etikett angegeben, um einen Ort in den Hautes-Alpes oder vielleicht um das bekannte Chamonix am Mont Blanc (Haute-Savoie) handelt, wodurch das bekannte Verbreitungsareal der Art beträchtlich erweitert würde.

VERTIKALVERBREITUNG : 1900-2400 m (FREINA & WITT, 1990).

BIOTOP : Alpine Kurzrasen (FREINA & WITT, 1990).

FLUGZEIT : Zweite Julihälfte bis August (FREINA & WITT, 1990). Vorliegende Funddaten vom 17. Juli bis 20. Juli.

Pharmacis anselminae (Teobaldelli, 1977)

UNTERSUCHTES MATERIAL : 16 ♂♂, Italia, Aosta, Valle di Valeille südlich von Lillaz (Cogne-Tal), 1900 m, 12.7.1990, leg. & coll. Kristal. 2 ♂♂, Italia, Aosta, Val di Champorcher, Umgebung Rifugio Dondena, 2000 m, 7.7.1991, leg. & coll. Kristal.

HABITUS (Abb. 4) : Spannweite 32-33,5 mm, Ø 32,6 mm (n = 6) ; TEOBALDELLI (1977) und FREINA & WITT (1990) : 28-33 mm. Vorderflügellänge 14,5-16,5 mm, Ø 15,1 mm (n = 18). Im Habitus erscheinen die Tiere untereinander recht einheitlich. Die Grundfärbung aller Flügel ist ein schwärzliches Dunkelbraun, in welchem auf den Vorderflügeln unregelmäßige, nicht scharf begrenzte, hellere, weißlichgraue Fleckchen stehen. Hellbraune Zeichnungselemente als Umrandung der helleren Flecken wie bei den anderen Arten der Gruppe fehlen gänzlich. Die Hinterflügel sind einfarbig dunkelbraun ohne Einmischungen, die Fransen aller Flügel sind ebenfalls einfarbig dunkelbraun.

MÄNNLICHER GENITALAPPARAT (Abb. 13-18) : Valven gebogen, kürzer als bei *Ph. claudiae*, in der Mitte etwas eingeschnürt, dadurch in der Form an eine Erdnuß erinnernd. Ventraler Rand des Vinculum regelmäßiger gerundet als bei *Ph. claudiae* aber kantiger als bei *Ph. bertrandi.* Vinculum zwischen den triangulären Fortsätzen in der Regel V-förmig eingebuchtet (zwei der untersuchten Männchen zeigen eine abweichende U-Form, Abb. 17-18) und ventral weniger stark ausgebuchtet. Vinculum stets mit fleckenartigen Sklerotisierungen entlang der Ränder (nur in Abb. 13 zeichnerisch dargestellt, aber in allen Präparaten vorhanden), die bei den anderen Arten fehlen. Pseudoteguminalplatte insgesamt ähnlich wie bei *Ph. claudiae*, das obere mediale Ende aber breit abgerundet, nur schwach sklerotisiert. Ventraler Rand der Juxta flach konkav gebogen. In der Vinculumform besteht eine gewisse Variation ; ferner zeigt ein Präparat (hier nicht abgebildet) im Vinculumbereich eine pathologische Deformation. Möglicherweise handelt es sich dabei um Defekte als Folge der Isolation (Inzucht).

Wir nutzen die Gelegenheit, die Genitalien von *Pharmacis anselminae* in Serie abzubilden. Die einzige bisher verfügbare Abbildung, das Foto eines ungünstig

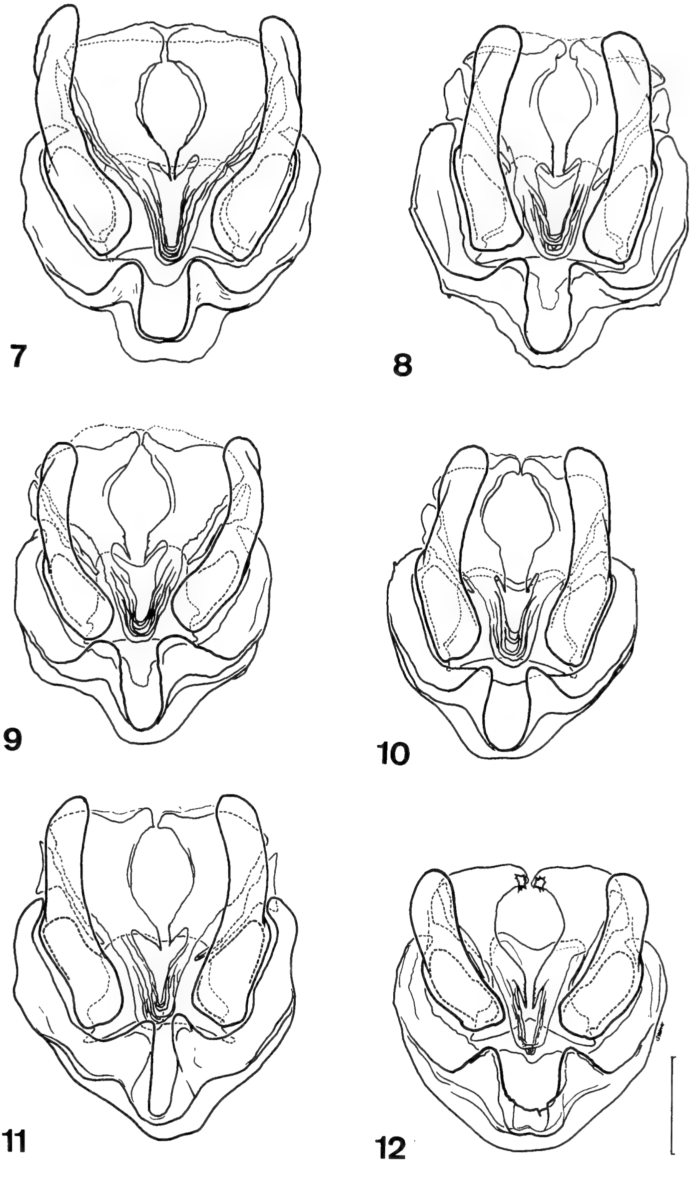

Abb. 7-12. Männliche Genitalien von *Pharmacis* spp. 7-11 — *Ph. claudiae* sp. n., Paratypen. Italien, Aosta, Valtournenche ; 12 — *Ph. bertrandi* (Le Cerf). Frankreich, Hautes Alpes, Chamonix. Maßstab 0,5 mm.

gelagerten Quetschpräparates zusammen mit einer unzulänglichen Beschreibung (TEOBALDELLI, 1977) hat die Beurteilung dieses Taxons eher erschwert als erleichtert und FREINA & WITT (1990) sogar zu der Vermutung veranlaßt, daß *anselminae* und *bertrandi* als konspezifisch aufzufassen seien.

WEIBCHEN : Die Weibchen sind brachypter (Abb. 5).

AKTIVITÄTSPHASE : 9-16 h mit Höhepunkt zwischen 10 und 12 h (TEOBALDELLI, 1977 ; 1979).

VERBREITUNG : Italienische Alpen, Aosta, bisher nur aus der Umgebung des oberen Cogne-Tals südlich des Valle d'Aosta bekannt : Valle di Valeille und Vallone di Urtier (Umg. Peradza) sowie Val di Champorcher (Umg. Dondena).

VERTIKALVERBREITUNG : 1800-2500 m (TEOBALDELLI, 1977 und eigene Beobachtungen) (3).

BIOTOP : Alpine Rasen oberhalb der Waldgrenze. Die bekannten Biotope sind z. T. stark beweidet.

FLUGZEIT : Anfang bis Mitte Juli von sehr kurzer Dauer. Nach den Angaben bei TEOBALDELLI (1977), den Funddaten der bei FREINA & WITT (1990) abgebildeten Tiere sowie den Belegstücken in der coll. Kristal vom 7. Juli bis 15. Juli.

Pharmacis carna ([Denis & Schiffermüller], 1775)

UNTERSUCHTES MATERIAL : 6 ♂♂, Italia, Trento/Brescia, Monte Tremalzo, 1800 m, Daten vom 27.7.-3.8.1974, leg. Ströhle, coll. Kristal.

HABITUS : Spannweite 32-37 mm, Ø 34,4 mm (n = 6) ; FREINA & WITT (1990) : ♂♂ 25-34 mm, ♀♀ 32-44 mm. Vorderflügellänge 15,5-17 mm, Ø 16,3 mm (n = 6). Die Grundfarbe der Flügel ist ein dunkleres Mittelbraun, in dem auf den Vorderflügeln unregelmäßige helle Zeichnungselemente stehen, die wiederum hellockerbraun umrandet sind. Vom Analwinkel ausgehend läuft eine aus ockerfarbenen Ringen bestehende Fleckenreihe direkt in den Apex des Vorderflügels. Die Fransen der Vorderflügel sind kaum erkennbar gescheckt, fast einfarbig mittelbraun, die Hinterflügelfransen sind am Grunde einfarbig dunkelbraun, an den Spitzen etwas heller gefärbt.

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(3) TEOBALDELLI (1977) machte verschiedene Aussagen. Die Daten der Typenserie lauten "bei 2000 m" bis "2500 m" ; im Text finden sich außerdem die Angaben "in Höhen zwischen 1800 und 2500 m" (S. 38) sowie "zwischen 1900 und 2200 m ... bei 2500 m" (S. 41).

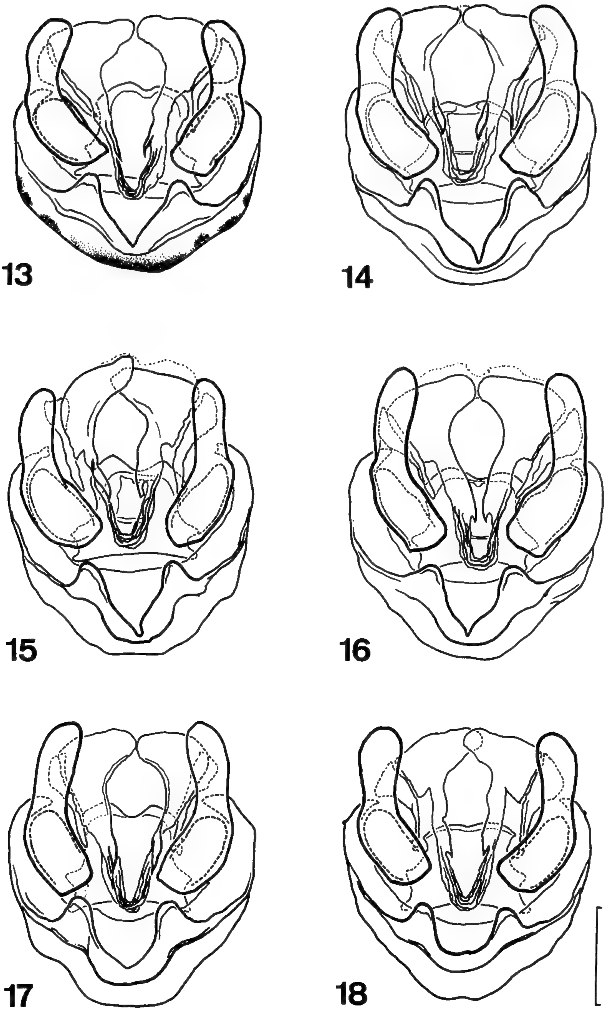

Abb. 13-18. *Pharmacis anselminae* (Teobaldelli), männliche Genitalien. Italien, Aosta, Val Cogne. Maßstab 0,5 mm.

Männlicher Genitalapparat (Abb. 19-20) : Valven länger und schlanker als bei *Ph. bertrandi* und *Ph. anselminae*, jedoch nicht so lang wie bei *Ph. claudiae*. Ventraler Rand des Vinculum konkav eingezogen, trianguläre Vinculumfortsätze schwächer ausgebildet als bei den Vergleichsarten, Einbuchtung zwischen den Fortsätzen flacher, breit U-förmig, wannenartig. Pseudoteguminalarme als zwei klappen-

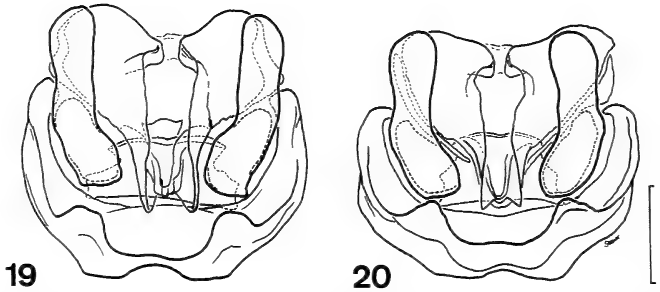

Abb. 19-20. *Pharmacis carna* (D. & S.), männliche Genitalien. Italien, Trento/Brescia, M. Tremalzo. Maßstab 0,5 mm.

artige Auswüchse ausgebildet, deren Form variiert. Der kleine, schneidenartige, sklerotisierte Fortsatz in der Mitte des medialen Randes der Pseudoteguminalplatte, der bei den Vergleichsarten vorhanden ist, fehlt bei *Ph. carna* völlig.

Weibchen : Die Weibchen haben voll entwickelte Flügel.

Aktivitätsphase : "*Hepialus carna* hat ein erstes Fluginterval im Morgengrauen, um welche Zeit einzelne ♂♂ — so ziemlich als letzte Falter — am Licht erscheinen. ... Die eigentliche Flugzeit setzt jedoch erst um 7.30 Uhr ein... Der Falter fliegt, so lange es ziemlich kühl ist, in der Sonne, etwa von 8.30 Uhr ab nur mehr an schattigen Stellen... Der Flug dauert bis gegen 12 Uhr..." (Daniel, 1950). Diese Beobachtungen beziehen sich auf Beobachtungen zwischen 1800 und 2200 m auf apinen Rasen an den Südhängen des Watzmannstockes in den Berchtesgadner Alpen. In tieferen Lagen konnte Daniel (1950) *Ph. carna* nur am Licht nachweisen.

Verbreitung : In Europa in den Alpen und den osteuropäischen Gebirgen. Ob sich die Angaben vom Ural und aus den asiatischen Gebirgen sowie aus den subarktischen Regionen Asiens wirklich alle auf *Ph. carna* beziehen, bedarf noch der Klärung, ebenso die bis heute in der Literatur vertretene Meldung aus der ungarischen Tiefebene (Pfitzner, 1912 ; Freina & Witt, 1990).

Vertikalverbreitung : In den Alpen von der montanen bis zur alpinen Höhenstufe. Daniel (1950) gibt für die Berchtesgadener Alpen Funde zwischen 1150 und 2200 m mit einem Maximum zwischen 1700 und 2000 m an. Die bei Freina & Witt (1990) abgebildeten alpinen Belegstücke weisen Funddaten zwischen 1300 und 1800 m auf. Ein Tier aus den Karpaten wird mit 540 m angegeben.

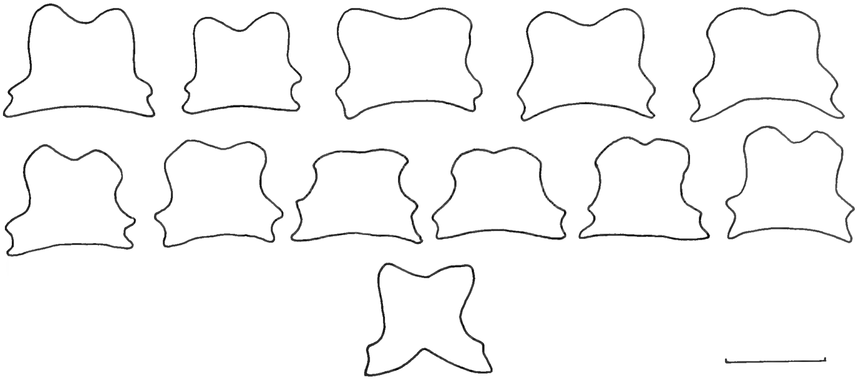

Abb. 21. Form der Juxta : obere Reihe *Pharmacis claudiae*, mittlere Reihe *Ph. anselminae*, untere Reihe *Ph. bertrandi*. Maßstab 0,5 mm.

Biotop : Montane und subalpine Populationen finden sich im Bereich üppigster Vegetation (Daniel, 1950). Freina & Witt (1990) verweisen auf kräuterreiche, hanglagige Wiesenmatten. Die alpinen Populationen bewohnen wie die verwandten Arten alpine Rasen.

Flugzeit : Ende Juni bis in den späten August (Freina & Witt, 1990).

Diskussion

(A. Steiner)

Ohne eine Gesamtrevision der Gattung *Pharmacis* lassen sich keine endgültigen Aussagen über die phylogenetische Stellung der einzelnen Taxa machen. *Ph. bertrandi* und *Ph. anselminae* stehen sich ungeachtet der klaren habituellen Unterschiede genitalmorphologisch sehr nahe ; möglicherweise sind sie Schwestertaxa. Es steht zu vermuten, daß die Brachypterie im weiblichen Geschlecht in der Gattung *Pharmacis* nur einmal aufgetreten ist, so daß alle Arten mit kurzflügeligen Weibchen ein Monophylum bilden und das Merkmal selbst eine Synapomorphie dieser Gruppe darstellt (als weitere Synapomorphien kommen die Merkmale "ventraler Rand des Vinculum ausgebuchtet" und "schneidenartiger sklerotisierter Fortsatz am medialen Rand der Pseudoteguminalplatte" in Frage).

Der weitgehende Verlust der Lokomotionsfähigkeit der weiblichen Imago durch Brachypterie ist ein schwerwiegender Schritt im Evolutionsgeschehen einer Art, der gut begründet sein muß. Die Brachypterie kann durch endogene Faktoren bedingt sein : die Weibchen einiger

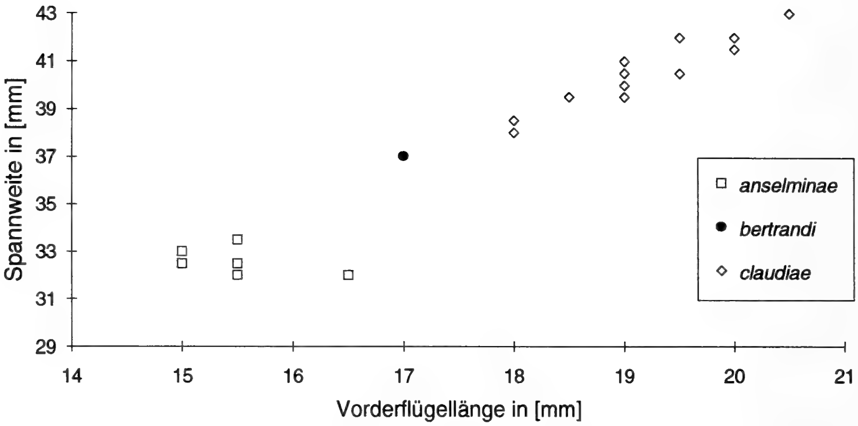

Abb. 22. Verhältnis von Vorderflügellänge und Spannweite.

Lasiocampiden und Arctiiden, die im Imaginalstadium keine Nahrung aufnehmen können und somit als Adulte nur eine kurze Lebensdauer haben, müssen bereits beim Schlupf den Großteil ihrer Eier fertig entwickelt haben. Durch das schwere Abdomen behindert sind solche Weibchen oft ausgesprochen flugträge und bewegen sich fast nur zu Fuß, so daß eine Flügelreduktion hier nur die Einsparung ohnehin ungenutzter Körperteile bedeutet. Als Ausgleich für die fehlende Vagilität der Weibchen haben dann meist die Raupen Ausbreitungspotentiale erschlossen, so bei *Orgyia* die Windverdriftung der L_1-Raupe, die dafür mit langen Haarbüscheln ausgestattet ist.

Brachypterie kann aber auch eine Reaktion auf exogene Faktoren sein, etwa bei Arten, die in ungünstigen Jahreszeiten fliegen (zahlreiche Herbst-, Winter- und Frühjahrsarten, besonders unter den Geometridae) oder in Regionen leben, in denen die Flugfähigkeit ein Nachteil sein kann, so im Falle von Endemiten auf kleinen Inseln in Gebieten mit starken Winden, die Gefahr laufen, aufs Meer verdriftet zu werden (z. B. *Agrotis cunhaensis*). Im Hochgebirge hat die Evolution der Brachypterie genau die selben Ursachen : Imagines von Arten, die die Glazialzeiten auf inneralpinen Nunatakkern — also ebenfalls in isolierter Lage — überdauerten, waren beim Verdriften von ihrer Refugiumsinsel auf die umliegenden Gletscher zum Tode verurteilt. Geringe Flugaktivität und in der Folge Flügelreduktion erwies sich in dieser Situation als Selektionsvorteil und wurde von einer ganzen Reihe von Arten genutzt, sowohl in den “massifs de refuge” der Hochgebirge als auch

Abb. 23. Habitat von *Pharmacis claudiae* sp. n. bei Antey-St.-André (Aosta).

im borealen Bereich (*Agrotis fatidica*, *Xestia (Schoyenia)* spp., *Elophos* spp., *Pharmacis* spp. u. a.). Doch was in den Glazialia eine Überlebensstrategie war, erweist sich heute als Hindernis für die Dispersion dieser Arten, so daß bei vielen von ihnen davon ausgegangen werden kann, daß ihr rezentes Areal sich seit dem letzten Glazial nur wenig erweitert hat. Ein auffallend geringes Dispersionspotential weisen auch manche flugfähigen Arten auf, z. B. einige Arten der Genera *Erebia*, *Psodos* und der Tribus *Gnophini*. (Daß die Flügelreduktion meist nur das weibliche Geschlecht betrifft, liegt daran, daß eine rasche Geschlechterfindung nur dann gewährleistet ist, wenn der suchende Partner geflügelt ist, und daß andererseits die Population den Verlust von Männchen eher verkraften kann, denn auch wenige überlebende Männchen sind in der Lage, alle vorhandenen Weibchen zu begatten, während jeder Verlust eines Weibchens den Verlust ihres Eivorrats und somit ihrer gesamten potentiellen Nachkommenschaft bedeutet.)

Die Gruppe der gebirgsbewohnenden *Pharmacis*-Arten mit brachypteren Weibchen wird im folgenden Text nach dem zuerst beschriebenen alpinen Vertreter als *bertrandi*-Artengruppe bezeichnet, umfaßt aber auch *Ph. pyrenaicus* (Donzel, 1838) und eventuell einen weiteren Vertreter im Kaukasus. Möglicherweise existieren noch unentdeckte oder bisher mit *Ph. carna* verwechselte Taxa in asiatischen Hochgebirgen. *Pharmacis carna* (eventuell einschließlich nahe verwandter geflügelter Arten) stellt vermutlich die Schwestergruppe der *Pharmacis bertrandi*-Gruppe dar. Im Laufe mehrerer Eiszeiten wurde das Areal der *Pharmacis bertrandi*-Gruppe mehrfach zersplittert und zweifellos sind auch manche Populationen, die den Vergletscherungen nicht ausweichen konnten, ausgestorben. Wann sich im alpinen Raum die Aufspaltung in die Arten *Ph. bertrandi*, *Ph. anselminae* und *Ph. claudiae* vollzogen hat, läßt sich beim heutigen Kenntnisstand nur schwer beurteilen ; die deutlichen Unterschiede in Habitus und Genitalmorphologie und die stark reliktäre Verbreitung lassen jedenfalls eine Aufspaltung schon vor dem Würmglazial vermuten. Die rezente Situation stellt sich folgendermaßen dar : Es existieren eine Reihe von isolierten Populationen im Bereich der Südwestalpen, wobei an jeder einzelnen Fundstelle nur je eines dieser Taxa nachgewiesen ist. Über ihr aktuelles Expansionspotential wissen wir wenig, die Weibchen sind aber flugunfähig und können wohl auch nicht von den Männchen transportiert werden ; als einzige Methode der Arealexpansion bleibt die Fortbewegung im Raupenstadium, und die dürfte bei terrestrischen Raupen, die nicht die Möglichkeit haben, sich im Jugendstadium am Faden treiben zu lassen, gering sein. Es sieht also so aus, als ob die einzelnen Populationen noch immer in etwa die Regionen bewohnen, die ihnen während des Höhepunkts des letzten Glazials als Refugien gedient haben. Zur Beurteilung der Frage, ob sich diese Populationen zu Arten differenziert haben, stehen derzeit folgende Informationen zur Verfügung : Habitus und Genitalmorphologie der Imagines (bei *Ph. claudiae* nur der Männchen), zirkadianer Aktivitätsrhythmus (nicht für alle Populationen), Flugzeit, Biotope und Vertikalverbreitung. Die zwei letzten Punkte sind bei allen Populationen so ähnlich, daß zur Beantwortung der Frage nur Morphologie, Anatomie, Flugzeit und tageszeitliche Aktivität bleiben. Bei den meisten Hepialidae besteht in großen und zusammenhängenden

Populationen in der Regel eine große Variation in der Flügelzeichnung und -färbung. Dies gilt für *Ph. fusconebulosa* (DE GEER, 1778) und darf wohl auch für den gemeinsamen Vorfahren der *Ph. bertrandi*-Artengruppe vorausgesetzt werden. Wenn bei einem solchen Vorfahren Engpässe (bottleneck-Situationen) in mehreren disjunkten Reliktpopulationen auftreten, wie dies während der Vereisungs- und Eisrückzugsphasen des Pleistozäns mehrfach eingetreten sein muß, dann darf geradezu damit gerechnet werden, daß sich die einzelnen disjunkten Teilpopulationen bezüglich des Merkmals Flügelzeichnung stark auseinanderentwickelten, so daß selbst nahestehende Taxa (z. B. Schwestertaxa) nicht unbedingt durch ähnliche Flügelzeichnung ausgezeichnet sein müssen und daß die Flügelzeichnung alleine in einer solchen Gruppe kein verläßlicher Indikator für genealogische Verwandtschaft sein kann. Differenzen in der Genitalmorphologie und in der tageszeitlichen Aktivität können hier eher zur Klärung verwandtschaftlicher Beziehungen herangezogen werden. Selbst in der Flugzeit scheinen sich *Ph. anselminae* und *Ph. claudiae* zu unterscheiden (wenn nicht sogar auszuschließen) : *Ph. anselminae* wurde nur bis zum 15.7., *Ph. claudiae* erst ab dem 28.7. nachgewiesen, wobei allerdings berücksichtigt werden muß, daß bisher für beide Arten nur wenige Phänologiedaten vorliegen.

Bei den geographisch teils sehr eng benachbarten Taxa der *Ph. bertrandi*-Gruppe bietet es sich an, durch Raupen- und Puppensuche oder Zucht einerseits die Präimaginalstadien kennenzulernen und deren Morphologie, Biologie und Ökologie zu vergleichen, andererseits virgine Weibchen zu erlangen und mit diesen in Biotopen der jeweils anderen Arten Anflugversuche durchzuführen, um das Vorhandensein (oder Fehlen) von Isolationsmechanismen durch Pheromoninkompatibilität, durch anatomische Differenzen in der Genitalmorphologie oder durch sich ausschließende zirkadiane Aktivitätsrhythmen nachzuweisen. Hier wie in ähnlich gelagerten Fällen öffnet sich ein weites Betätigungsfeld auch für den Amateur-Entomologen, der sich nicht auf das Anhäufen toter Imagines beschränken sollte, sondern — mit entsprechender wissenschaftlicher Untermauerung — wertvolle Beiträge zur Kenntnis der Holomorphe und ihrer Autökologie liefern kann. Schließlich muß mit der Möglichkeit gerechnet werden, daß in den südwestlichen Alpen (besonders auf der entomofaunistisch wenig intensiv durchforschten italienischen Seite) weitere lokale Populationen von Vertretern der *Ph. bertrandi*-Artengruppe existieren, die noch ihrer Entdeckung harren.

Danksagung

Wie danken Herrn Thomas Witt (München) für die Ausleihe eines *Pharmacis bertrandi*-Belegstücks und Herrn Wolfgang Ströhle (Weiden/Opf.) für die Überlassung einer Serie von *Pharmacis carna*.

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Die Puppen der Tribus Cyclophorini Mitteleuropas (Lepidoptera : Geometridae)

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Summary

The pupae of the central European species of the tribe Cyclophorini (Lepidoptera, Geometridae) — The pupae of 11 species of Central European Cyclophorini (Lepidoptera, Geometridae, Sterrhinae) are characterised, described and figured. A key for the determination of pupae of the genus *Cyclophora* Hübner and some biological data are added. The current system within the genus *Cyclophora* is discussed on the basis of pupal characters.

Zusammenfassung

Die Puppen von 11 Arten der mitteleuropäischen Cyclophorini (Lepidoptera, Geometridae, Sterrhinae) werden charakterisiert, beschrieben und abgebildet. Eine Tabelle zur Bestimmung der Arten der einzigen mitteleuropäischen Gattung *Cyclophora* Hübner und einige bionomische Angaben werden beigefügt. Das derzeitige System der Gattung *Cyclophora* wird anhand der Puppenmerkmale diskutiert.

Résumé

L'auteur caractérise, décrit et figure les chrysalides de 11 espèces de Cyclophorini d'Europe centrale (Lepidoptera, Geometridae, Sterrhinae). Il présente en outre un tableau de détermination pour les espèces du seul genre d'Europe centrale : *Cyclophora* Hübner, et ajoute quelques données sur la bionomie. Discussion du système actuel de classement dans le genre *Cyclophora* sur la base des caractères des chrysalides.

Diese Arbeit knüpft an Patočka (im Druck) an und behandelt die Puppen der Cyclophorini (Lepidoptera, Geometridae, Sterrhinae) mit der einzigen mitteleuropäischen Gattung *Cyclophora* Hübner. Das System und die Nomenklatur folgen Leraut (1980), die morphologische Terminologie (vgl. Abb. 1, 2) Mosher (1916) und McGuffin (1967).

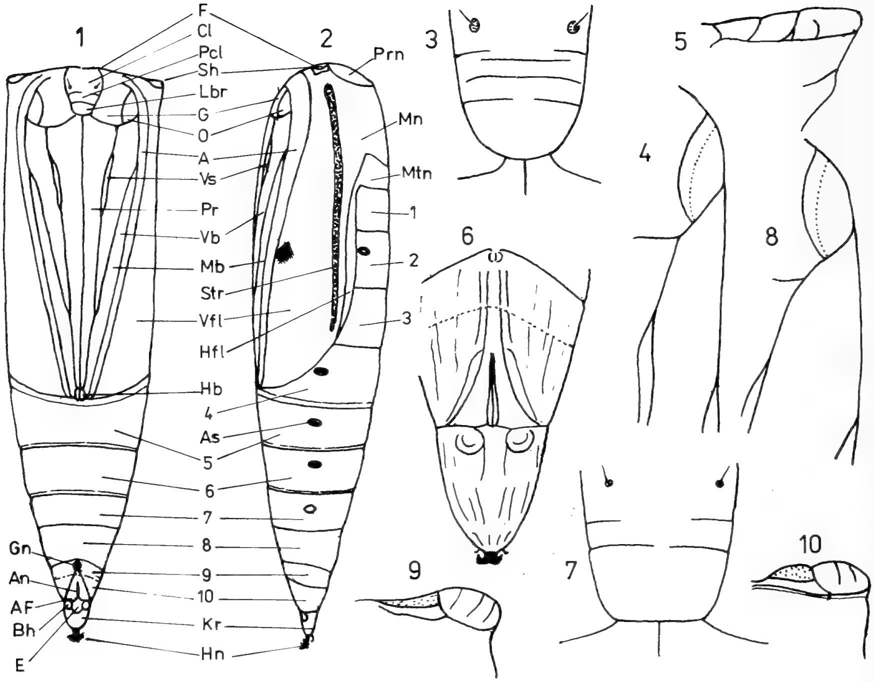

Abb. 1-10. 1-2 — *Cyclophora* sp. ; 3-7 — *C. pendularia* ; 8-9 — *C. albiocellaria* ; 10 — *C. annulata*.
1 — Habitusbild in Ventral- ; 2 — in Lateralansicht ; 3, 7 — Clypeus, Labrum ; 4, 8 — Oculi und Umgebung ; 5, 9, 10 — thorakaler Spiracularhöcker.
A = Antennae, Af = Analfeld, An = Analnaht, As = abdominale Spiracula, Bh = Basalhöcker, Cl - Clypeus, E = Einsenkung, F = Frons, G = Genae, Gn = Genitalnaht, ♂, Hb = Hinterbeine, Hfl = Hinterflügel, Hn = Häkchen, Kr = Kremaster, Lbr = Labrum, Mb = Mittelbeine, Msn = Mesonotum, Mtn = Metanotum, O = Oculi, Pcl = Postclypeus, Pr = Proboscis, Prn = Pronotum, Sh = Spiracularhöcker, Str = Streifen im Analteil der Vorderflügel, Vb = Vorderbeine, Vfl = Vorderflügel, Vs = Vorderschenkel, 1-10 = 1.-10. Abdominalsegment.

Tribus Cyclophorini

Diese Tribus enthält in Mitteleuropa nur die Gattung *Cyclophora* Hübner, 1822, mit folgender Charakteristik :

Mittelkleine (ca. 11-14 × 2,5-3,5 mm), ziemlich gleichförmige, in Ventralsicht charakteristisch keilförmige Spannerpuppen (Abb. 1), vorn am breitesten und stark abgestumpft. Thorakale Spiracularhöcker eckenartig vorspringend. Von diesen läuft parallel zum Dorsalrand der Vorderflügel je eine erhabene Kante. Auch zwischen Clypeus und Frons eine Kante (Abb. 1-2). Färbung fahl (sand-) gelb bis rot- oder graubräunlich. Manche Arten weisen außerdem grüne Puppenformen auf. Körper oft gesprenkelt mit Fleckenzeichnungen am Clypeus, an der Vorderflügelbasis, am Thorax und Abdomen. Längs des kantenartigen Dorsalteiles der Vorderflügel oft ein dunkler Streifen, auch die Adern manchmal ± verdunkelt. Puppen nur schwach glänzend. Skulptur mittelgrob bis mittelfein, wirr runzelig, zuweilen etwas höckerig, 1.-7. Abdominalsegment meist mit — scharfen Punktgrübchen (Abb. 18, 45). Labrum breit, abgerundet bis trapezförmig (Abb. 3, 7, 20). Labium ganz verdeckt. Genae oben beulenartig erhaben. Die Grenze zwischen Proboscis und Genae verläuft eher quer zur Längsachse der Puppe, die zwischen den Vorderbeinen und Antennae mehr schräg. Grenze der Vorderbeine mit den Antennae 4-5 × länger, die mit den Genae etwa 1,5-3 × kürzer als die Grenze zwischen den Vorderbeinen und Oculi (Abb. 4, 8). Vorderschenkel und Enden der Hinterbeine sichtbar. Proboscis wenig, Vorderbeine deutlich kürzer als die Mittelbeine und Antennae, diese überragen die Vorderflügel nicht (Abb. 1). Basen der Antennae, Frons, der ziemlich gut differenzierte, schmale Vertex und das Pronotum befinden sich an der abgestumpften Frontalseite der Puppe (Abb. 2). Frontolateral (Spiracular-) Höcker des Mesonotums manchmal mit komplizierten Einschnürungen, zuweilen lappig (Abb. 9, 43). Frontolaterale Ausläufer des Metanotums relativ spitz (Abb. 19, 39). Thorakale Spiracula undeutlich. Hinterflügel schmal, bis etwa zum Caudalrand des 3. Abdominalsegmentes sichtbar. Spiracula am 2. Abdominalsegment deutlich, am 3. Segment verdeckt, relativ groß, elliptisch, ihre Höfe breit (Abb. 2). Zwischen dem 9. und 10. Abdominalsegment, dorsal und lateral, gibt es weder eine Rinne, noch Einschnitte (Abb. 11, 12). Das 9. Segment ziemlich kurz, insbesondere an der Ventralseite. An der Dorsalseite trägt es V- oder trapezförmige, zuweilen abgerundete Vertiefungen, die kantenartig gesäumt sind (Abb. 11, 12, 27, 31, 33). Analfeld deutlich, meist dreieckig, manchmal längsgefurcht. Die Analnaht zuweilen mit erhabenen Lateralwällen (Abb. 17, 22).

Kremaster ± so lang wie basal breit, dorsoventral abgeplattet. In der Dorsalansicht ist er entweder zungenförmig, am Ende relativ spitz (Abb. 33) ; oder am Ende abgestumpft (Abb. 12), bzw. stumpf- oder rechtwinklig (Abb. 31, 42). Ventralseite oft mit Basalhöckern und einer größeren oder kleineren Basalvertiefung (Abb. 6, 17). Von den 4 Paaren der hakenartigen Kremasterborsten entspringt D1 dorsal vor dem Ende des Kremasters und ist kleiner als die übrigen. Diese etwa gleichgroß, dicht in einer Gruppe am Kremasterende konzentriert (Abb. 54). Sonst ist der Kremaster ± gerunzelt bzw. gefurcht.

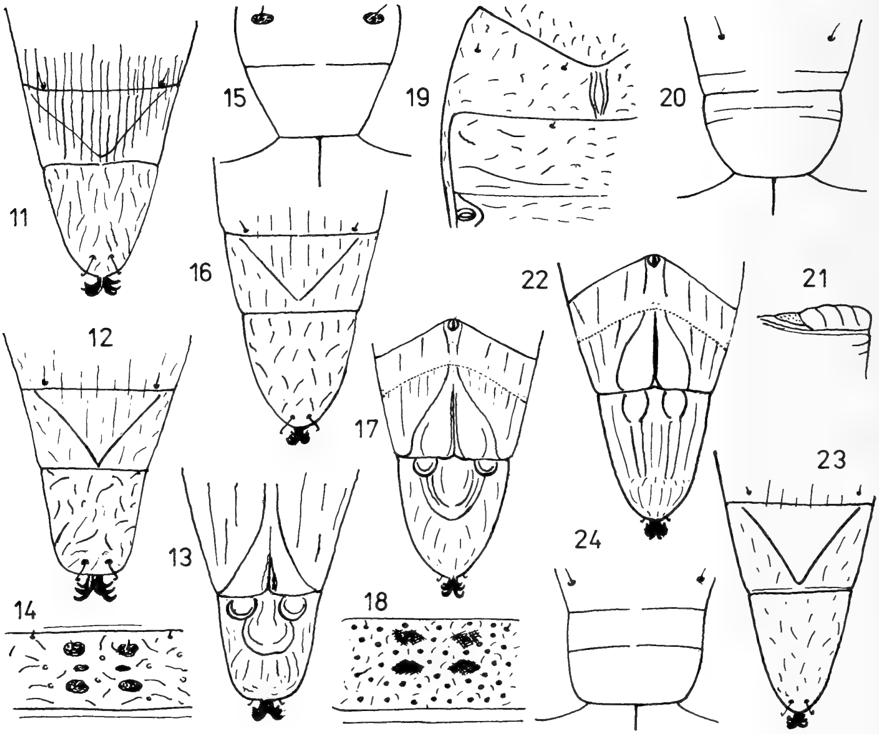

Abb. 11-24. 11 — *Cyclophora pendularia* ; 12-14 — *C. albiocellaria* ; 15-18 — *C. annulata* ; 19-23 — *C. albipunctata* ; 24 — *C. puppillaria.*
11, 12, 16, 23 — Abdomenende in Dorsal- ; 13, 17, 18 — in Ventralsicht ; 14, 18 — 5. Abdominalsegment in Dorsalsicht ; 15, 20, 24 — Labrum, Clypeus ; 21 — thorakaler Spiracularhöcker.

Die Puppe ruht oberirdisch an einem besponnenen Blatt der Futterpflanze, mit Hilfe der Kremasterhäkchen und eines Gespinstgürtels "tagfalterartig" am Blatt befestigt. Die Überwinterung findet im abgefallenen Laub bzw. in einer noch belaubten Baumkrone statt. Die Arten leben vorwiegend an Laubhölzern (nur *C. suppunctaria* an Kräutern) und sind in Mitteleuropa meist bivoltin (selten uni- bzw. trivoltin) ; die Puppen findet man im Sommer und von Herbst zum Frühling. Die einzelnen Arten bewohnen Laub- und Mischwälder, zuweilen die Waldsteppe. *C. puppillaria* ist als Wanderfalter bekannt. Wirtschaftlich sind sie fast bedeutungslos.

Bestimmungstabelle der Arten

1 Dorsal am 10. Abdominalsegment eine keilförmige (dreieckige) Vertiefung (Abb. 11, 23, 38), zuweilen durch die Längsfurchung verdeckt und weniger scharf (Abb. 11) **2**

— Dorsal am 10 Abdominalsegment eine trapezförmige (an der Caudalseite abgestumpfte) Vertiefung (Abb. 27, 31, 33) **7**

2(1) Die Vertiefung dorsal am 10. Abdominalsegment unscharf, durch scharfe Längsfurchung verdeckt (Abb. 11). Puppenfärbung trüb braungrau .... ***C. pendularia***

— Die Vertiefung dorsal am 10. Abdominalsegment scharf (Abb. 23, 54). Körperfärbung sandbraun, gelbbraun bis trüb strohgelb, manchmal auch grün **3**

3(2) Seiten der Vertiefung dorsal am 10. Abdominalsegment stark geschwungen, Spitze spitzwinklig vorgezogen (Abb. 38) :........ ***C. quercimontaria***

— Seiten der Vertiefung dorsal am 10. Abdominalegment nicht oder kaum geschwungen, Spitze deshalb nicht vorgezogen (Abb. 12,54) **4**

4(3) Vorderflügel mit einem dunklen Fleck in der Mitte (Abb. 2). Kremaster in Dorsalsicht meist allmählich zungenförmig zugespitzt (Abb. 23) .... ***C. annulata***

— Vorderflügel ohne einen dunklen Fleck in der Mitte. Kremaster in Dorsalsicht meist erst im Endteil abgerundet, oder stumpf- bis rechtwinklig zugespitzt (Abb. 12, 16, 54) **5**

5(4) Dunkle Sprenkelung und Flecken an Borstenbasen am Thorax und Abdomen fehlend (Abb. 19). Labrum abgerundet trapezförmig (Abb. 20) .... ***C. albipunctata***

— Dunkle Sprenkelung und Flecken am Thorax und Abdomen deutlich (Abb. 14, 55, 56). Labrum trapezförmig (Abb. 7,51) **6**

6(5) Labrum mit wenig schrägen Seiten, dunkle Flecken an der Basis der Clypealborsten klein, punktförmig (Abb. 7). Kremaster in Ventralsicht mit einer tiefen, breiten Vertiefung im Basalteil, am Ende stumpf abgerundet (Abb. 13) .... ***C. albiocellaria***

— Labrum mit schrägen Seiten, dunkle Flecken an der Basis der Clypealborsten relativ groß (Abb. 51). Kremaster in Ventralsicht mit schwacher, eher länglicher Vertiefung, am Ende meist stumpf- bis rechtwinklig (Abb. 53) .... ***C. linearia***

7(1) Vertiefung dorsal am 10. Abdominalsegment im Caudalteil breit (manchmal u-förmig abgerundet), Caudalrand nicht kürzer als die Lateralränder (Abb. 27, 33) **8**

— Vertiefung dorsal am 10. Adominalsegment im Caudalteil schmal, Caudalrand viel kürzer als die Lateralränder (Abb. 31, 42, 47) **9**

8(7) Labrum — halbkreisförmig (Abb. 35). Grenze der Vorderbeine mit den Genae etwa 3 × kürzer als die mit den Oculi (Abb. 4). Kremaster in Ventralsicht mit deutlichen Basalhöckern. Analfeld groß, breit, Lateralwälle der Analnaht nicht stark hervortretend (Abb. 29). Vertiefung am 10. Abdominalsegment dorsal mit ± scharfen Ecken (Abb. 33) .... ***C. porata***

— Labrum ± abgerundet viereckig (Abb. 24). Grenze der Vorderbeine mit den Genae kaum 2 × kürzer als die mit den Oculi (Abb. 8). Basalhöcker an der Ventralseite des Kremasters kaum angedeutet, Analfeld schmal, Analnaht mit starken Lateralwällen (Abb. 25). Vertiefung am 10. Abdominalsegment dorsal mit ± abgerundeten Ecken (Abb. 27) .... ***C. puppillaria***

9(7) Puppe mit gut entwickelter dunkelbrauner Fleckenzeichnung dorsal am Thorax und Abdomen (Abb. 45). Clypeale Borsten auf dunklen Basalflächen (Abb. 44) .... ***C. punctaria***

— Puppe ohne oder mit ganz schwacher Fleckenzeichnung (Abb. 48). Clypealborsten höchstens auf dunklen Punkten (Abb. 46) **10**

10(9) Puppe fahlbraungelb oder rötlichgelb gefärbt. Skulptur, besonders an den Vorderflügeln (auch an deren Basis) ziemlich fein. Labrum lateral gewölbt. Caudalseite gerade (Abb. 28). Lateralränder der Dorsalvertiefung am 10. Abdominalsegment — einwärts gebogen (Abb. 31) .... ***C. ruficiliaria***

— Puppe fahl braungrau gefärbt. Skulptur gröber, z.T. höckerig. Labrum auch an der Caudalseite gewölbt (Abb. 46). Lateralränder der Dorsalvertiefung am 10. Abdominalsegment auswärts gebogen (Abb. 47) .... ***C. suppunctaria***

Cyclophora pendularia (Clerck, 1759)

5 ♂, 5 ♀ aus der Slowakei und aus Böhmen wurden untersucht. Puppe schlank mit spitzem Abdomenende. Färbung bräunlich hellgrau, dunkle Zeichnung an den Vorderflügeln spärlich, dunkel braungrau. Punkte an der Basis der Clypealborsten etwas größer, sonst dorsal am Thorax und Abdomen klein, unauffällig. Skulptur am Notum und Abdomen wirr gerunzelt, Punktgrübchen an den mittleren Abdominalsegmenten unscharf. Labrum an der Caudalseite — abgerundet (Abb. 3). Grenze der Vorderbeine mit den Oculi etwa 2 × länger als die mit den Genae (Abb. 8). Spiraculare Ausläufer am Thorax stark hervortretend mit feinen Einschnürungen, wenig gelappt (Abb. 9). Vertiefung dorsal am 10. Abdominalsegment keilförmig, hinten in etwa rechtwinklig, unscharf, durch starke Längsfurchung weniger auffällig (Abb. 11). Analfeld schlank dreieckig, Seitenwälle schwach, sonst Umgebung längsgerunzelt (Abb. 6). Kremaster wenig länger als basal breit, zum Ende zungenförmig verschmälert, am Ende abgerundet, wirr gerunzelt. Basalhöcker an der Ventralseite deutlich, dazwischen fast keine Vertiefung. Häkchen relativ klein, dunkel graubraun (Abb. 6, 11). Raupe an *Salix* spp., seltener an verschiedenen anderen Laubhölzern. Laubholzbestände an Gewässerufern, mehr in tieferen Lagen, lokal.

Cyclophora albiocellaria (Hübner, 1789)

3 ♂, 4 ♀ aus der Slowakei wurden untersucht. Puppe ziemlich gedrungen, hell sandgelb, deutlich und scharf schwarzbraun gezeichnet. Rückenfleckchen dick (Abb. 14). Punktgrübchen an mittleren Abdominalsegmenten ziemlich tief, unscharf. Labrum stumpf trapezförmig mit steilen Seiten (Abb. 7). Grenze der Vorderbeine mit den Oculi kaum 2 × länger als die mit den Genae (Abb. 8). Thorakale Spircularausläufer relativ stumpf (Abb. 9). Vertiefung dorsal am 10. Abdominalsegment scharf, keilförmig, Seiten wenig geschwungen, Spitze nicht vorgezogen (Abb. 12). Analfeld dreieckig, Seitenwälle der Analnaht niedrig. Sonst Ventralseite des 10. Abdominalsegmentes längsgefurcht. Kremaster meist etwas länger als basal breit, am Ende abgerundet. Ventralseite stark vertieft, Endteil längsgefurcht, sonst Furchung eher wirr. Ba sal höcker deutlich. Häkchen relativ stark und dick, braun (Abb. 12, 13).

Raupe an *Acer* spp. In der Waldsteppe und Randzone der Waldbestände an warmtrockenen Standorten im Süden und Südosten Mitteleuropas.

Cyclophora annulata (Schulze, 1775)

5 ♂, 5 ♀ aus der Slowakei wurden untersucht. Puppe relativ klein, ziemlich gedrungen, meist unscharf gezeichnet, u.a. ein charakteristischer dunkler Fleck an den Vorderflügeln (Abb. 2), dunkle dorsale Fleckchen am Thorax und Abdomen fließen oft streifenartig zusammen. An den mittleren Abdominalsegmenten tiefe, relativ scharfe Punktgrübchen (Abb. 18). Labium trapezförmig mit schrägen Seiten (Abb. 15). Grenze der Vorderbeine mit den Oculi mehr als 2 × länger als die mit den Genae. Thorakale Spircularhöcker relativ stumpf, schwächer gewölbt als bei *C. albiocellaria* (Abb. 10). Dorsalvertiefung am 10. Abdominalsegment derjenigen der vorigen Art ziemlich ähnlich (Abb. 16), ebenso das Analfeld und der Kremaster, dieser ist jedoch spitzer. Endhäkchen relativ stark, braun (Abb. 16, 17).

Raupen an *Acer* spp., seltener an anderen Laubhölzern. Randzone der Laubwälder, Gebüsch. An mäßig feuchten bis trockenen Standorten wärmerer Lagen, verbreitet.

Cyclophora albipunctata (Hufnagel, 1767)

5 ♂, 5 ♀ Puppen aus der Slowakei und aus Böhmen wurden untersucht. Puppe ziemlich gedrungen, sandgelbbraun oder grün, Flügelstreifen oft scharf, schwarzbraun, Fleck im Mittelteil der Vorderflügel nicht vor-

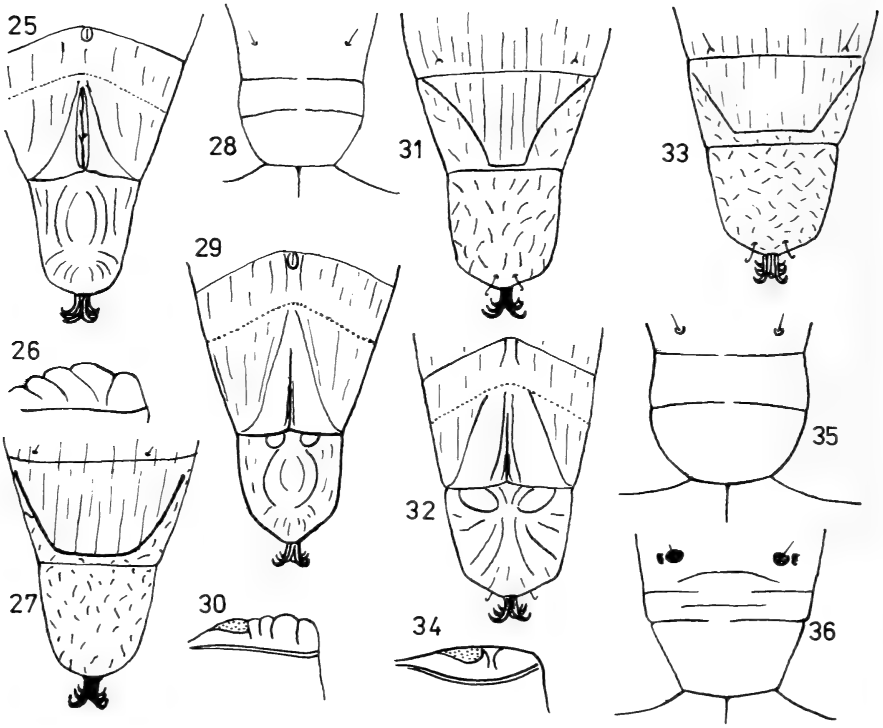

Abb. 25-36. 25-27 — *Cyclophora puppillaria* ; 28-31 — *C. ruficiliaria* ; 32-35 — *C. porata* ; 36 — *C. quercimontaria.*
25, 29, 32 — Abdomenende in Ventralsicht ; 26, 30, 34 — thorakaler Spiracularhöcker ; 27, 31, 33 — Abdomenende in Dorsalsicht ; 28, 35, 36 — Labrum, Clypeus.

handen. Wurzel-Punkte der Clypealborsten schwach (Abb. 20). Fleckenzeichnungen am Thorax und Abdomen reduziert oder fehlend (Abb. 19). Morphologisch jedoch *C. annulata* ähnlich. Labrum abgerundet trapezförmig (Abb. 20), Grenze der Vorderbeine mit den Oculi mehr als 2 × länger als die mit den Genae (Abb. 4). Thorakale Spiracularhöcker mehr hervortretend, der große äußere Teil gewölbt, mit Einschnürungen (Abb. 21). Analfeld mit stärker hervortretenden Wällen. Kremaster an der Ventralseite kaum vertieft, Basalhöcker angedeutet. Häkchen ziemlich klein, braun (Abb. 22, 23).

Raupe an *Betula* spp., auch an *Alnus* spp., seltener an anderen Laubhölzern. In Birkenhainen, Laub- und Mischwäldern an Gewässerufern.

Cyclophora puppillaria (Hübner, 1799)

2 ♀ aus Frankreich (Coll. Staudinger, Museum für Naturkunde, Berlin) wurden untersucht. Färbung nach Forster & Wohlfahrt (1981) "dunkelgrün mit einigen hellen Linien auf dem Rücken und an den Rändern der Flügelscheiden. Kopfspitzen und Kremaster leicht weinrot", möglicherweise jedoch auch braungelb. Exuvie trüb strohgelb, Abdomenende mehr bräunlich, Zeichnungen praktisch fehlend. Punktgrübchen nicht allzu stark. Labrum mit geschwungenen Seiten, Clypealborsten ohne dunkle Punkte (Abb. 24). Grenze zwischen den Vorderbeinen und Oculi etwa 2 × länger als die zwischen Vorderbeinen und Genae. Thorakale Spiracularhöcker schwächer hervortretend, lappig (Abb. 26). Das 10. Abdominalsegment dorsal mit einer sehr breiten trapezförmigen Vertiefung, deren Ecken ± abgerundet sind. Caudalrand nicht kürzer als die Lateralränder (Abb. 27). Analnaht lang mit ± deutlichen Seitenzweigen, Lateralwälle stark, Analfeld schmal, dreieckig. Kremaster an der Ventralseite ohne deutliche Basalhöcker, Basalteil vertieft, Endteil eher angeschwollen. Dorsalseite wirr gerunzelt. Ende des Kremasters abgerundet (Abb. 25, 27).

Raupe in Mitteleuropa angeblich an *Quercus* spp. An trockenwarmen Standorten im äußersten Süden Mitteleuropas (und im Mediterrangebiet), als Wanderfalter auch weiter nordwärts vordringend.

Cyclophora ruficiliaria (Herrich-Schäffer, 1855)

2 ♂, 2 ♀ Puppen aus der Slowakei wurden untersucht. Abdomenende relativ schlank. Färbung fahlgelb, Zeichnung stark reduziert bzw. fast fehlend. Vorderflügel höchstens mit einem schmalen Analstreifen oder mit schwach verdunkelten Adern. Punkte an Borstenbasen (auch die der Clypealborsten, Abb. 28) meist kaum sichtbar. Skulptur an den Vorderflügeln, auch an deren Basis, ziemlich fein. Punktgrübchen an den mittleren Abdominalsegmenten verhältnismäßig scharf. Labrum breit, Seiten gewölbt (Abb. 28). Grenze der Vorderbeine mit den Oculi ± zweimal länger als die der Oculi mit den Genae. Thorakaler Spiracularhöcker mittelstark hervortretend, gewölbt, mit scharfen Quereinschnürungen (Abb. 30). 9. und 10. Abdominalsegment dorsal längsgefurcht. Dorsalvertiefung am 10. Segment scharf begrenzt, schmal trapezförmig, Seitenränder schräg, viel länger als der Caudalrand und etwas einwärts geschwungen (Abb. 31). Analnaht mit schwachen Seitenwällen, Analfeld groß. Kremaster relativ kurz, breit, Ventralseite mit angedeuteten Basalhöckern und einer breiten Vertiefung. Kremaster vor dem Ende etwas angeschwollen. Dorsalseite relativ stark, wirr gefurcht.

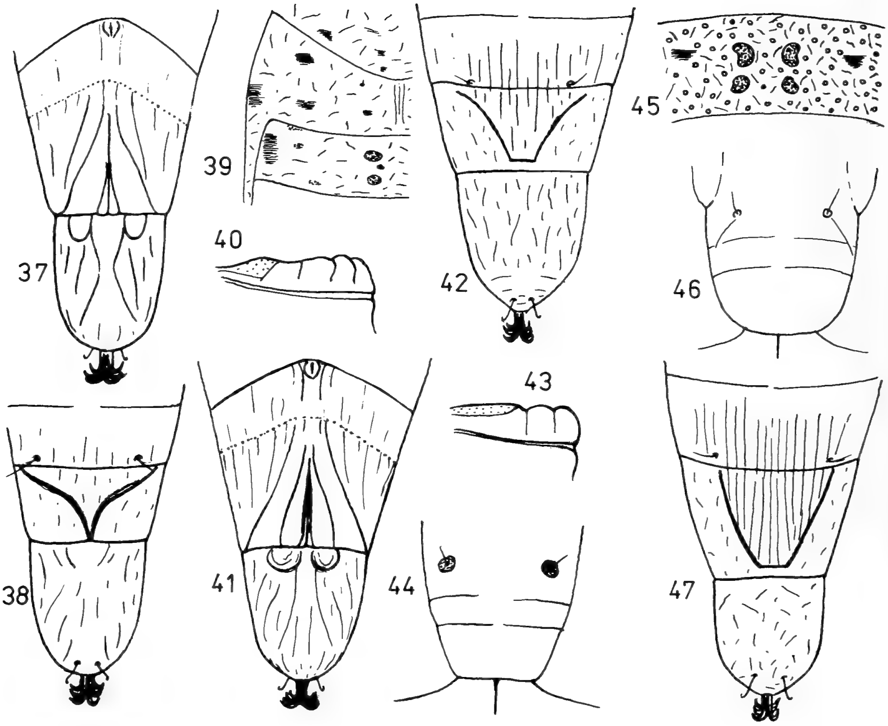

Abb. 37-47. 37-40 — *Cyclophora quercimontaria* ; 41-45 — *C. punctaria* ; 46-47 — *C. suppunctaria*.
37, 41 — Abdomenende in Ventral- ; 38, 42, 47 — in Dorsalsicht ; 39 — Metanotum, 1. Abdominalsegment, limke Seite ; 40, 43 — thorakaler Spiracularhöcker ; 44, 45 — Labrum, Clypeus ; 45 — 5. Abdominalsegment in Dorsalsicht.

Das Ende in Dorsalansicht etwas winkelförmig. Häkchen stark, rotbraun (Abb. 31, 32).

Raupe an *Quercus* spp. (in der Slowakei wird *Q. cerris* bevorzugt). Lokal an trockenwarmen Standorten.

Cyclophora porata (Linnaeus, 1767)

1 ♂, 1 ♀ Puppe aus dem Naturhistorischen Museum Wien wurden untersucht. Färbung gelbbräunlich, Exuvie trüb strohgelb. Zeichnung reduziert. Vorderflügel nur mit etwas dunkleren Adern. Thorax und Abdomen fast ohne dunkle Sprenkelung. Punkte an der Borstenbasis (auch an den Clypealborsten, Abb. 35) kaum dunkler. Punktgrübchen am Abdomen unscharf, nur in der Umgebung der Spiracula deutlicher.

Labrum breit abgerundet, Ränder (auch der Caudalrand) gewölbt (Abb. 35). Grenze der Vorderbeine mit den Genae kurz (fast 3 × kürzer als die mit den Oculi, vgl. Abb. 4). Thorakale Spiracularhöcker mittelstark erhaben, mäßig gewölbt, Einschnürungen schwach (Abb. 34). Dorsale Vertiefung am 10. Abdominalsegment breit trapezförmig, eckig, Seiten schräg, Caudalrand kaum kürzer als die Lateralränder (Abb. 33). Analfeld relativ breit, Analnaht mit mäßigen Lateralwällen. Kremaster relativ kurz, vor dem Ende stumpfwinklig oder quer zur Längsachse abgestumpft. Ventralseite mit schwachen Basalhöckern, dazwischen vertieft ; sonst nur mäßig, Dorsalseite deutlicher, skulpturiert. Häkchen ziemlich kräftig (Abb. 32, 33).

Raupe an *Quercus* spp., *Betula* spp., vorzugsweise auf sandigen Böden, in Heiden u. dgl.

Cyclophora quercimontaria (Bastelberger, 1897)

5 ♂, 5 ♀ Puppen aus der Slowakei wurden untersucht. Puppe mäßig gedrungen, oft dunkel braungrau gesprenkelt, Flügeladern ± verdunkelt, dunkle Fleckchen an der Basis der Borsten (Abb. 39). Exuvie hell sand- bis strohgelb, Abdomenende oft dunkler. Punktgrübchen mittelscharf. Labium breit trapezförmig, Caudalrand meist konvex (zuweilen auch konkav). An der Basis der Clypealborsten die dunklen Fleckchen deutlich (Abb. 36). Grenze der Vorderbeine mit den Genae mehr als zweimal kürzer als die mit den Oculi (vgl. Abb. 4). Thorakale Spiracularhöcker mittelstark, mäßig eingeschnürt und gelappt (Abb. 40). 10. Abdominalsegment dorsal mit einer tiefen, keilartigen Vertiefung, Seiten geschwungen, Spitze spitzwinklig, vorgezogen (Abb. 38). Analfeld mit schwachen Lateralwällen. Kremaster meist länger als basal breit, zum Ende verjüngt, am Ende selbst abgerundet. Ventralseite mit starken Basalhöckern, dazwischen vertieft, Endteil längs-, Dorsalseite eher wirr gefurcht. Häkchen stark, rotbraun (Abb. 37, 38).

Raupe an *Quercus* spp., lokal, an trockenwarmen Standorten (Waldsteppen, Heiden). Bevorzugt buschige Eichen.

Cyclophora punctaria (Linnaeus, 1758)

5 ♂, 5 ♀ aus der Slowakei wurden untersucht. Puppe ziemlich gedrungen, sandfarben, seltener grün, ähnlich wie die vorige scharf gezeichnet (Abb. 45). Labrum trapezförmig mit schrägen, meist geraden Seiten, am Caudalrand manchmal etwas ausgeschnitten. Fleckchen an der Basis der Clypealborsten deutlich (Abb. 44). Grenze der Vorderbeine mit den Oculi mehr als 2 × länger als die mit den Genae (vgl. Abb. 4).

Thorakaler Spiracularhöcker mittelstark erhaben mit deutlichen Einschnürungen (Abb. 43). Dorsalvertiefung am 10. Abdominalsegment (im Unterschied zu der sonst ähnlichen vorigen Art bzw. zu *C. linearia*) schmal trapezförmig, Caudalrand viel kürzer als die schrägen, kaum geschwungenen Seitenränder (Abb. 42). Analfeld schlank dreieckig. Lateralwälle der Analnaht ziemlich erhaben. Kremaster kaum oder wenig länger als basal breit, vor dem Ende in Dorsalsicht zugespitzt. Ventralseite mit Basalhöckern und einer meist kleinen, oder fehlenden Vertiefung. Dorsalseite mäßig gerunzelt. Häkchen mittelstark, rotbraun (Abb. 41, 42).

Raupe an *Quercus* spp. In Eichenwäldern aller Art oft häufig.

Cyclophora suppunctaria (Zeller, 1847)

5 ♂, 5 ♀ aus der Slowakei wurden untersucht. Der *C. ruficiliaria* morphologisch ähnlich. Unterscheidet sich durch die mehr fahl graubraune Färbung (*C. ruficiliaria* ist eher fahlgelb), durch die gröbere und teilweise auch höckerige Skulptur an Thorax, Abdomen- und Vorderflügelbasis (Abb. 48). Punktgrübchen am Abdomen meist weniger scharf. Abgrenzung des Labrums — lateral und auch caudal — gewölbt (Abb. 46). Das 9. und 10. Abdominalsegment dorsal längsgefurcht. Am 10. ist eine trapezförmige Vertiefung, deren Seiten ein bißchen auswärts gebogen sind. Caudalrand viel kürzer als die Seitenränder (Abb. 47). Das Abdominalsegment ventral und auch das Analfeld längsgefurcht (Abb 50 ; stärker als bei *C. ruficiliaria*). Kremaster ventral kaum konkav mit ± starken Basalhöckern, wirr gefurcht — auch an der Dorsalseite. Kremasterende in Dorsalsicht ± stumpf bis rechtwinklig zugespitzt, Häkchen mittelstark, dunkel rotbraun (Abb. 47, 50).

Raupe an Kräutern wie *Artemisia campestris*, *Hippocrepis* spp., *Melilotus* spp. An trockenwarmen Standorten, z.B. Waldsteppen im südöstlichen Mitteleuropa, lokal.

Cyclophora linearia (Hübner, [1799])

5 ♂, 5 ♀ Puppen aus der Slowakei wurden untersucht. Der *C. punctaria* ähnlich, ± rötlich braunsandgelb, Sprenkelung und Flecken am Clypeus, Thorax und Abdomen und Streifen an den Vordeflügeln meist scharf (Abb. 51, 55, 56). Punktgrübchen am Abdomen relativ deutlich. Labrum trapezförmig (Abb. 51). Grenze der Vorderbeine mit den Oculi wenigstens 2 × länger als die mit den Genae (vgl. Abb. 4). Thorakale Spiracularhöcker stark hervortretend, Einschnürungen jedoch kaum angedeutet (Abb. 52). 9. und 10. Abdominalsegment dorsal — gerunzelt.

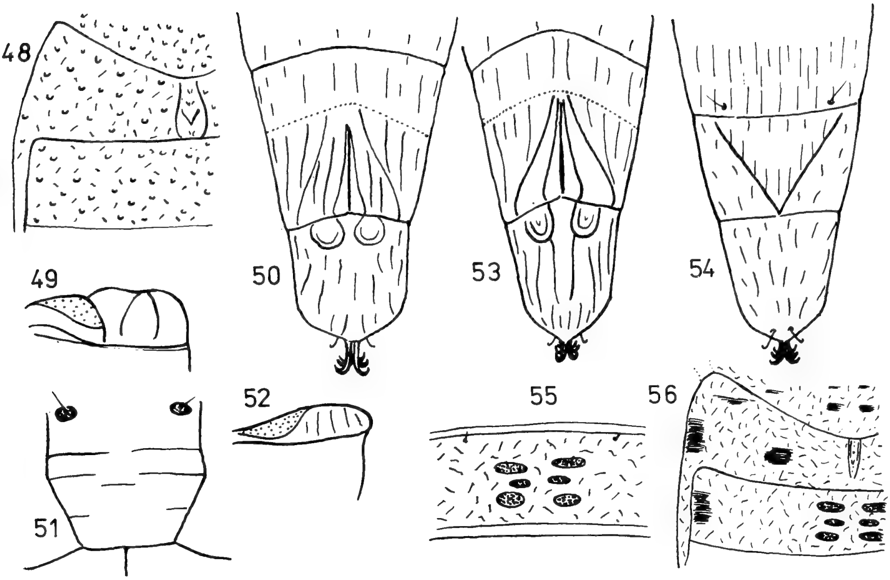

Abb. 48-56. 48-51 — *Cyclophora suppunctaria* ; 52-56 — *C. linearia*.
48, 56 — Metanotum, 1. Abdominalsegment ; 49, 52 — thorakaler Spiracularhöcker ; 50, 53 — Abdomenende in Ventralsicht ; 51 — Labrum, Clypeus ; 54 — Abdomenende in Dorsalsicht ; 55 — 3. Abdominalsegment in Dorsalsicht.

Am 10. Abdominalsegment eine spitz keilförmige Vertiefung mit wenig oder nicht geschwungenen Seiten (Unterschied gegenüber *C. quercimontaria*) und kaum vorgezogener Spitze (Abb. 54). Analfeld deutlich, Ränder der Analnaht oft wallartig erhaben. Kremaster meist etwas länger als basal breit ; Ventralseite meist mit deutlichen Basalhöckern und einer Vertiefung. Kremasterendteil in Dorsalsicht etwas zugespitzt. Häkchen ziemlich stark, rotbraun (Abb. 53, 54).

Raupe an Laubhölzern, vorzugsweise an *Fagus sylvatica* und *Quercus* spp., auch an *Vaccinium* spp., bevorzugt Eichen-Buchen-Wälder, dort oft häufig.

Diskussion

Die untersuchten Puppen der Tribus Cyclophorini mit der einzigen mitteleuropäischen Gattung *Cyclophora* bilden hinsichtlich ihres Baues eine geschlossene, wenig differenzierte Einheit. Auch die einzelnen, auf Grund ihrer bevorzugten Futterpflanzen gebildeten Gruppen — an Salicaceae (*C. pendularia*), Betulaceae (*C. albipunctata*), Fagaceae

(*C. puppillaria*, *C. ruficiliaria*, *C. porata*, *C. quercimontaria*, *C. punctaria*, *C. linearia*), Aceraceae (*C. albiocellaria*, *C. annulata*), Asteraceae, Fabaceae u.a. (*C. suppunctaria*) unterscheiden sich puppenmorphologisch kaum voneinander.

Die *Cyclophora*-Puppen weichen von den anderen der Familie Geometridae stark ab. Ihre Körperform ist der bei den Spannern wenig üblichen Verpuppungsweise an der Oberfäche der Blätter ihrer Nahrungspflanzen angepaßt und weist dementsprechend weitgehende Adaptationen auf. Sie entsprechen anderen, sich auf diese Weise verpuppenden (und sonst einander wenig verwandten) Schmetterlingsgruppen. Auffallend ist der lang vorgezogene Kremaster mit der Konzentrierung der hakenförmigen Haftborsten auf sein Caudalende. Eine sonst bei der Familie Geometridae wenig übliche, helle Färbung, nicht selten mit Zeichnungen, fast ohne Glanz, eckige Ausläufer am Vorderteil des Körpers, die Befestigung der Puppe an einem Blatt mittels Kremasterhäkchen und eines Gespinstgürtels erinnern an ähnliche Verhältnisse bei den Familien Papilionidae, Pieridae usw. Während die einzelnen Arten auch als Imagines relativ schwer zu bestimmen sind, ist ihre Unterscheidung anhand der Puppenmerkmale möglich und relativ verläßlich.

Danksagung

Der Verfasser dankt mehreren Fachkollegen, insbesondere Doz. Dr. Z. Laštůvka (Brünn), Ing. J. Skyva (Prag), dem Museum für Naturkunde in Berlin (Dr. W. Mey) und dem Naturhistorischen Museum in Wien (Dr. M. Lödl) für die Überlassung bzw. Ausleihe des Puppenmaterials zur Untersuchung.

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Une nouvelle espèce européenne du genre *Pancalia* Stephens (Lepidoptera : Cosmopterigidae, Antequerinae)

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Summary

A new European species of the genus *Pancalia* Stephens (Lepidoptera, Cosmopterigidae, Antequerinae) — *Pancalia baldizzonella* sp. n. is described from southern Italy. Adults and genitalia of both sexes are illustrated. The new species is most closely related to *P. latreillella* Curtis and *P. nodosella* (Bruand), from which it can be distinguished by the wing markings and genitalic characters.

Résumé

Description de *Pancalia baldizzonella* sp. n. d'Italie méridionale. Les adultes et les armures génitales des deux sexes de ce taxon sont figurées.

Zusammenfassung

Pancalia baldizzonella sp. n. wird aus Süditalien beschrieben. Die Imagines und die Genitalien beider Geschlechter werden abgebildet. Die neue Art steht *P. latreillella* Curtis und *P. nodosella* (Bruand) am nächsten, von denen sie sich durch die Flügelzeichnung und Genitalmerkmale unterscheidet.

Introduction

Depuis la parution d'un article de Gaedike (1967) consacré aux espèces de *Pancalia* Stephens, 1829, ce genre et ses espèces ont été étudiés à plusieurs réprises (Leraut, 1984 ; Riedl, 1984 ; Sinev, 1985). Ces études ont permis d'expliquer la position systématique du genre en question et de confirmer, après deux révisions, l'existence de 9 espèces nominales habitant uniquement la zone paléarctique, à savoir *P. gaedikei* Sinev, 1985, *P. hexachrysa* (Meyrick, 1935), *P. isshikii* Matsumura, 1931, *P. latreillella* Curtis, 1830, *P. leuwenhoekella* (Linnaeus, 1761), *P. nodosella* (Bruand, [1851]), *P. sichotella* Christoph, 1882, *P. sinense* Gaedike, 1967, *P. swetlanae* Sinev, 1985.

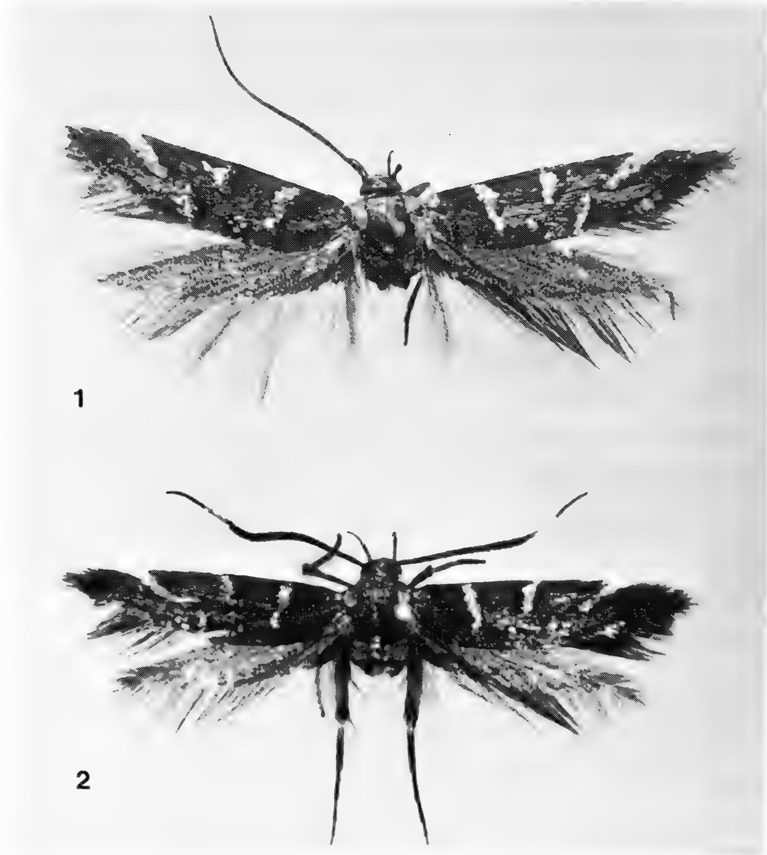


Fig. 1-2. *Pancalia baldizzonella* sp. n. 1 — holotype (mâle) ; 2 — paratype (femelle) (phot. G. Baldizzone).

Il m'a récemment été possible d'examiner les matériaux récoltés par le Dr. G. Baldizzone en Italie méridionale et de trouver parmi de nombreux Cosmopterigidae une nouvelle espèce du genre *Pancalia* qui est donc le dixième taxon spécifique appartenant à ce genre.

***Pancalia baldizzonella* sp. n.**

Holotype (Fig. 1) : Mâle, "Mt. Pollino, 1500 m, Lucania, Piano di Ruggio, 9. VII. 1991, G. Baldizzone leg.", prép. gén. no. 1415/R.
Paratype (Fig. 2) : Femelle, prép. gén. no. 1414/R. Portant la même étiquette. L'holotype et le paratype sont conservés dans la collection du Dr. G. Baldizzone à Asti.

Envergure de l'holotype : 15 mm ; du paratype : 14,5 mm. Tête, thorax, tegulae et palpes labiaux brun foncé, unicolores, brillants. Antennes brun foncé, unicolores chez le mâle et avec la partie subterminale du flagellum blanche chez la femelle (Fig. 1-2).

Ailes antérieures foncées ; la base, l'apex, les bords antérieur et postérieur sont brun foncé, la partie centrale de l'aile est brun-jaunâtre. Le dessin se compose d'une tache costale externe blanche et de tubercules d'écailles réfractives argentées. Le bord antérieur présente trois tubercules dont l'externe est réuni avec la tache costale blanche et l'interne, réuni avec le tubercule postérieur interne, forme avec celui-ci une écharpe transversale basale. Le second tubercule postérieur est rond, petit et situé plus près de la base de l'aile que le tubercule costal intermédiaire. Le troisième est allongé, enfin le quatrième, étroit, peu développé, est situé le long du bord postérieur de l'aile sous le tubercule costal externe et la tache costale blanche. Franges brun foncé. Ailes postérieures et leurs franges brun foncé.

La forme des bandes du système de renforcement de la base de l'abdomen (Fig. 3) est la même que chez *P. latreillella* Curtis : la bande transversale est droite, mince, les bandes latérales du premier tergite sont également à peu près droites.

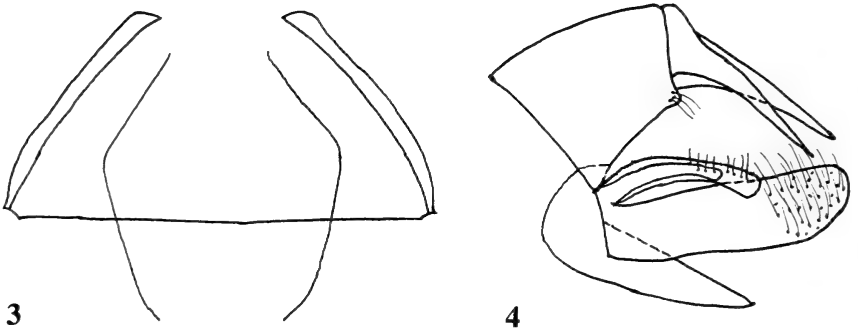
ARMURE GÉNITALE MÂLE (Fig. 4-6) : Valves lobiformes, non arquées, leur bord ventral légèrement concave. Juxta développée en tant que deux bras de longeur inégale (Fig. 5), allongés et étroits. Aedoeagus arqué (Fig. 6) ; sa partie proximale possède une saillie ventrale très distincte. Terminaison de l'aedoeagus aiguë.

ARMURE GÉNITALE FEMELLE (Fig. 9) : Lamelle antévaginale à bords latéraux parallèles, son bord proximal convexe. Ostium bursae étroit, les deux signa peu distincts.

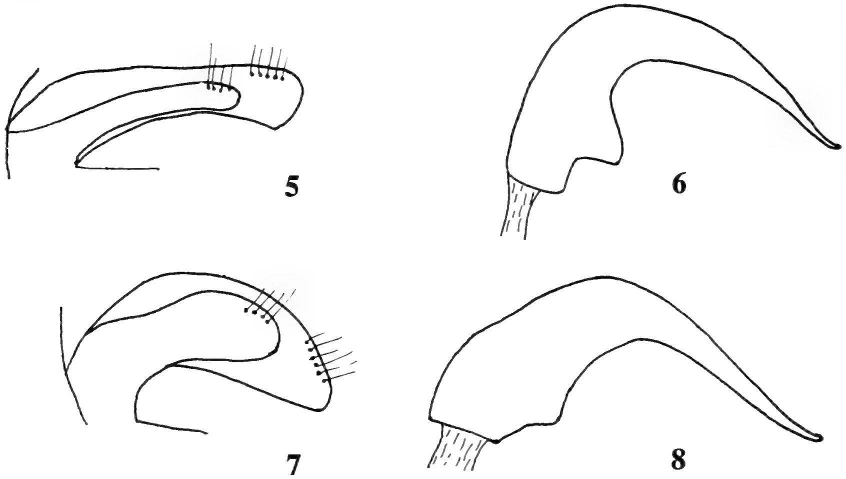
Je nomme cette intéressante nouvelle espèce européenne en l'honneur de mon éminent collègue italien, distingué spécialiste des Lépidoptères Coleophoridae, le Dr. Giorgio Baldizzone (Asti).

Commentaire

P. baldizzonella sp. n. est la plus proche de deux espèces européennes, *P. latreillella* Curtis et *P. nodosella* (Bruand). Elle s'en distingue cependant au premier coup d'œil par le fond de la partie centrale des ailes antérieures qui est brun-jaunâtre tandis que chez les deux espèces mentionnées ce fond est ferrugineux foncé. Le dessin des ailes antérieures ne présente aucun caractère particulier. Les différences les plus marquées concernent la forme des armures génitales. Chez le mâle, les deux bras



Figs 3-4. *Pancalia baldizzonella* sp. n. 3 — système de renforcement ; 4 — armure génitale mâle.



Figs 5-8. *Pancalia* spp., armure génitale mâle : bras de la juxta (5, 7) ; aedoeagus (6, 8). 5, 6 — *P. baldizzonella* sp. n. ; 7, 8 — *P. nodosella* (Bruand).

de la juxta (Fig. 5) sont relativement étroits et allongés ; chez d'autres espèces de *Pancalia*, par example chez *P. nodosella* (Bruand) (Fig. 7), ces sclérites sont moins allongés et nettement plus larges. En outre, parmi toutes les espèces connues de *Pancalia*, *P. baldizzonella* sp. n. présente la saillie ventrale de l'aedoeagus la plus grande (Fig. 6). Cette saillie chez les autres, y compris *P. nodosella* (Bruand) (Fig. 8), est plus petite et moins distincte. Chez la femelle, notre attention doit se porter sur la forme de la lamelle antévaginale, qui est bien caractéristique et diffère sensiblement de celles d'autres espèces de *Pancalia*.

Fig. 9. *Pancalia baldizzonella* sp. n., armure génitale femelle.

En ce qui concerne la localité-type de *P. baldizzonella* sp. n., il s'agit du Massif Mont Pollino (Lucanie, Italie méridionale) ; Piano di Ruggio se trouve dans une grande prairie située dans le Massif en question.

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Aufruf zur Mitarbeit

Die Schmetterlinge der Schweiz und ihre Lebensräume

Verbreitungskarten (5 × 5 km Netz) der 'Spinner und Schwärmer' der Schweiz werden für eine Fortsetzung des inzwischen sehr bekannten und geschätzten Buches 'Tagfalter und ihre Lebensräume' vorbereitet.

Um diese Verbreitungskarten zu ergänzen, sind alle Lepidopterologen eingeladen, uns ihre Schweizer Funddaten dieser Falter mitzuteilen. Bearbeitet werden alle Macrolepidopteren Familien, einschliesslich der Psychidae und Hesperiidae, aber ohne die Papilionoidea und (vorläufig noch) die Noctuidae und Geometridae.

Gewünscht sind mindestens : Fundort, -datum und -stadien von einwandfrei bestimmtem Material. Zusatzinformationen wenn möglich : Kanton, CH-Koordinaten, Sammler, ob Belegstück vorhanden, Sammlung, Raupenfutterpflanze.

Ich werde die Daten sammeln und an die einzelnen Familien-Bearbeiter zur Kontrolle weiterleiten. Daten für die Sesiidae und Thyrididae bearbeite ich selbst. Daten von schwierig zu bestimmenden Arten werden eventuell nicht berücksichtigt, oder nur nach Genitaluntersuchung, wie z.B. bei den meisten Zygaeniden. Die kontrollierten Daten werden in die Databank des Schweizerischen Zentrum für die kartographische Erfassung der Fauna (SZKF, CSCF) in Neuchâtel aufgenommen. Lepidopterologen welche uns Verbreitungsdaten mitteilen werden im Buch erwähnt.

Für die lepidopterologische Arbeitsgruppe der Schweiz,

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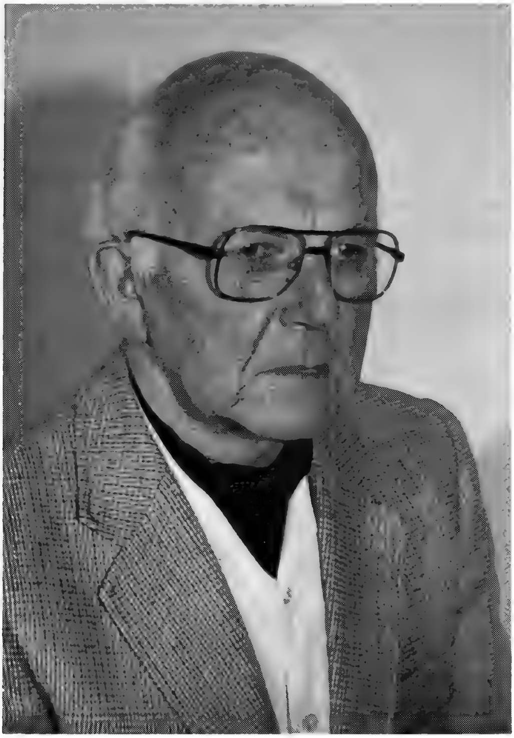
Ing. Eberhard Jäckh †
(1902-1993)



Am 22. August 1993 verstarb Eberhard Jäckh in seinen Haus in Hörmanshofen. Er saß in seinem Sessel, als er schnell und fast schmerzlos zur ewigen Ruhe kam.

Er wurde am 5. Dezember 1902 in Kassel geboren, hat also den größten Teil dieses ausgehenden Jahrhunderts erlebt. Zur Zeit seiner Geburt regierte noch der Kaiser in Deutschland und der "Weltkrieg" war noch kein Begriff. Autos standen noch am Anfang der Entwicklung, Rundfunk und Fernsehen waren unbekannt, wie die meisten Geräte der heutigen Technik.

Eberhard war das älteste von drei Geschwistern, Sohn von Dr. med. Alexander Jäckh, Chirurg und Frau Erna, geb. Hartdegen, einer talentierten Malerin.

Die Eltern starben beide früh. Schon während seiner Studienjahre im Internat entdeckte Eberhard jene Begeisterung für Insekten, die für sein ganzes Leben bestimmend wurde. Die Berufsausbildung begann er in Bremen, mit der Idee, als Schiffsingenieur die Welt kennenzulernen. Nach Abschluß der Ausbildung am Technikum erwies sich jedoch, daß seine immer größer werdende Passion für die Entomologie nicht mit wochenlangen Fahrten auf hoher See zu vereinbaren waren. So wechselte er über zum Flugzeugbau. Viele Jahre arbeitete er bei der Firma Focke Wulf in Bremen, was ihm die direkte Teilnahme am ganz Europa zerstörenden Krieg ersparte. Auch seine Wohnung in Bremen wurde zerstört. 1937 heiratete er Adele Lakmann. 1940 wurde ein Sohn, auch Eberhard benannt, geboren, der jetzt mit seiner Familie in den USA lebt.

Sein Interesse an der Entomologie vertiefte sich. Er konnte seine Kenntnisse erweitern, dank der Zusammenarbeit mit einigen bekannten Insektenforschern. Besonders Prof. E. M. Hering, Berlin, wurde sein Lehrmeister und Freund. Vor allem widmete er sich den Microlepidopteren. Äußerst aktiv beteiligte er sich am Wiederaufbau des Entomologischen Vereines Bremen. Das Bremer Überseemuseum engagierte ihn zunächst als freien Mitarbeiter. Das Hobby wurde zum Beruf, als ihm gleich nach dem Krieg 1945 die Leitung der Entomologischen Abteilung des Museums übertragen wurde, die er bis zur Pensionierung behielt (1967).

Seine Frau Adele verstarb früh in Jahre 1960. Sieben Jahre später heiratete er Ingeborg Hoyer, die ihn als liebevolle Gefährtin bis zu seinem letzten Atemzuge begleitete. 1974 zogen beide von Bremen zum Alpenrand und erwarben ein Haus in Hörmanshofen im Allgäu.

Das Ehepaar ist viel gereist, vor allem nach Italien. Beide sprachen italienisch, liebten die Sonne, das Mittelmeer und die üppige farbenfrohe Natur, die oft Thema ihrer anderen Passion, der Fotografie, wurde. Ihr beliebtestes Reiseziel war immer Ligurien, die Riviera dei Fiori. Dort “entdeckten” sie Conna, eine winzige Ortschaft, eine Gruppe von steinernen Häusern, gelegen an den Ausläufern des Apennin, eingetaucht in Pinien, Ginster und Buschwald. Dort verbrachten sie viele Wochen und sammelten reiche menschliche und naturwissenschaftliche Erfahrungen. Bedeutsam waren auch ihre Reisen in die USA, wobei die interessanten entomologischen Forschungen verbunden waren mit den Zusammentreffen mit der Familie des Sohnes.

Eberhard Jäckh verbrachte seine letzten Lebensjahre zu Hause in Hörmanshofen gestärkt durch die Liebe seiner Frau und seiner kleinen Enkelin Giannina, die viel in seiner Nähe war und viel von ihm gelernt hat. Er genoß ihre zärtliche Liebe, die wohl dazu beigetragen hat ihn bis ins 92. Lebensjahr aufrecht zu halten.

In der Entomologie gehört Eberhard Jäckh zu den bedeutenden deutschsprachigen Forschern, die die Grundlage für die moderne Lepidopterenforschung gebildet haben. Er hat seine während der Studienjahre gewonnenen technologischen Erkenntnisse für die entomologischen Forschungen benutzt und dabei neue Lösungen und hervorragende Ergebnisse erzielt. Unter anderem machte er technische Experimente für den Nachtfang. Durch eine Reihe von Versuchen kam es zur Erfindung einer leichten sehr wirksamen tragbaren Lampe, die er auch für Kollegen anfertigte.

Als einer der ersten wandte er die Methode der Artenbestimmung durch die Untersuchung der Genitalien an. Mehr als 11 000 mikroskopische Präparate wurden mit den verschiedensten Färbetechniken angefertigt, um besonders scharfe Fotos davon zu erhalten. Denn auch die Mikrofotografie wurde mit Sorgfalt betrieben, bearbeitet im eigenen, sinnvoll mit einfachen Mitteln eingerichteten Labor, assistiert von seiner Frau, die professionelle Fotografin ist.

So sind seine ganzen Forschungen durch Bilder belegt. Er hinterläßt ein eindrucksvolles Archiv, das aus über 20 000, nach der systematischen Mikrolepidopterenordnung klassifizierten Bildern besteht. Dabei sind auch ca. 100 Corodia-Filme, die Schmetterlinge in ihrer natürlichen Umwelt zeigen, sowie ca. 1 000 Schwarzweißfilme. Jede studierte Art ist dokumentiert im Entwicklungsstadium, wenn möglich in der Natur, mit Genitalfotos beider Geschlechter, in Variationen, sowie manchmal mit Fotos der Larve oder der Spuren an der Futterpflanze.

Die Sammlung Jäckh ist von sehr hohem wissenschaftlichen Wert. Sie umfaßt ca. 75 000 perfekt präparierte und etikettierte Exemplare, sorgfältig geordnet in großen, von Jäckh selbst gefertigten Holzkästen. Der Hauptkern besteht aus europäischem Material, sowie einer großen Anzahl in Nordamerika gesammelter Exemplare.

Manche Exemplare wurden gezüchtet, um die Biologie der Microlepidopteren zu beobachten, vor allem der "Minierer", wie Nepticulidae, Lyonetiidae, Gracillariidae und Coleophoridae. Dazu gibt es auch eine wichtige Sammlung von sorgfältig katalogisierten minierten Blättern.

Die Bibliothek enthält ca. 150 Bände, teils seltene Exemplare, mit Widmungen und Notizen der Autoren sowie ca. 2000 Sonderdrucken von Entomologen der ganzen Welt. Die gesamte Sammlung wurde schon vor Jahren dem Smithsonian Institution in Washington, USA, übereignet, das somit eine der wichtigsten und weltbekanntesten Privatsammlungen bekam.

Jäckhs wissenschaftliche Veröffentlichungen sind nicht so zahlreich, weil er die große Menge seiner Erkenntnisse immer sehr vorsichtig darstellte. Aber die, die er hinterlassen hat, sind von hohem wissenschaftlichen Wert meistens durch

Fotos dokumentiert. Somit ist Jäckh einer der ersten Autoren, der der guten Fotografie, zwecks besserer Objektivität, den Vorzug vor der Zeichnung gab.

Im Laufe seiner Tätigkeit hat Jäckh verschiedene Gruppen und Familien der Lepidopteren bearbeitet (Gracillariidae, Lyonetiidae, Gelechiidae, Coleophoridae, Tortricidae, Pterophoridae, etc.), was seine umfangreichen Kenntnisse über Microlepidopteren beweist. Unter anderem hat er eine Revision der Gattung *Batia* Stephens und *Pseudatemelia* Rebel (Oecophoridae) vorgenommen. In den letzten Jahren hat er sich auf die Familie der Scythrididae spezialisiert und einige wichtige Beiträge erbracht mit der Revision verwandter Gruppen und der Beschreibung neuer Arten.

Mit großer Bescheidenheit hat er nach 1978 mit der Veröffentlichung seiner wissenschaftlichen Arbeit aufgehört, um "altersbedingte Fehler" zu vermeiden. Fortgesetzt hat er seine Arbeiten im Archiv, welches viele neue Arten, sowie Arten der Gattung *Scythris* enthält, die auf eine Beschreibung warten. Eine der ihn begeisternden Gruppen war die *Alucita*, über die er die Basis für eine komplette Revision der palearktischen Fauna vorbereitet hat. Glücklicherweise ist diese Arbeit nicht verloren. Wieder aufgenommen und ergänzt von Jäckhs jungem "Schüler" Axel Scholz, ist sie vor kurzem veröffentlicht worden.

Ich habe Eberhard Jäckh 1973 in Conna kennengelernt. Damals entstand zwischen uns eine brüderliche Freundschaft, mit gegenseitigen Besuchen und gemeinsamen wissenschaftlichen Forschungen an der Riviera, auf den Hügeln des Monferrato, auf dem Monte Baldo, der Insel Krk, etc. Wir verbrachten miteinander viele unvergeßliche Stunden. Wir suchten Raupen und minierte Blätter, saßen neben der brennenden Lampe an einem xerothermischen Hang, diskutierten unaufhörlich über die Natur, planten Forschungen, Exkursionen und Publikationen. Aber oft sprachen wir auch über das Leben und die Geschichte dieses Jahrhunderts, das er selbst dahinfließen sah. Ich verdanke Eberhard den größten Teil meiner Kenntnisse über Microlepidopteren. Besonders über alles, was ich über die Technik der Mikroskopie, Mikrofotografie, und der Sammlungs- und Lichtfangmethoden weiß. Alles wurde mir mit großer Geduld und Hingabe erklärt, voller Sympathie und Großherzigkeit.

Aber viel verdanke ich ihm auch von einem menschlichen Gesichtspunkt aus. Es war eine echte Lebensschule mit unvergeßlicher Korrektheit, Ehrlichkeits-, Zähigkeits-, Freundlichkeits-, Bescheidenheitslehren und einer riesigen Liebe zur Natur.

Giorgio BALDIZZONE

Liste der Publikationen

1927. Zur Entwicklung von *Gracillaria azaleella* Brants. *Anz. Schädlingsk.* 3 : 53-54.
1933. Über einige das nordwestdeutsche Faunengebiet kennzeichnende Micro-Lepidopteren. *Mitt. ent. Ver. Bremen* 21 : 6-10.
1934. Zur Überwinterung des Zitronenfalters, *Gonepteryx rhamni* L. *Kosmos* 31 : 31-32, 1 Abb.
1936. Bemerkungen über *Trichoptilus paludum* Z. *Mitt. ent. Ges. Halle* 14 : 5-7.
1940. Die Insekten des Naturschutzparkes des Lüneburger Heide, III. Die Kleinschmetterlinge (Microlepidoptera). *Abh. naturw. Ver. Bremen* 31 : 786-806, 4 Abb.
1942. Die Microlepidopteren-Fauna des rechtsseitigen Mittelrheintales nebst Beschreibung von *Borkhausenia magnatella* spec. nov. (Lep. Gelechiidae). *Z. wien. EntVer.* 27 : 137-141, 174-200, 216-221, 230-241, 3 Abb., 1 Taf.
1951. *Pristophora florella* (Mann, 1862) (Pyralidae, Phycitinae) am Mittelrhein. *Z. Lepid.* 1 : 105.
1951. Bemerkenswerte Lepidopterenfunde auf Wangeroog in den Jahren 1947, 1949 u. 1950. Beschreibung der Raupe von *Agdistis bennetii* Curt. *Z. Lepid.* 1 : 121-122.
1951. Praktische Genitalpräparate. *Z. Lepid.* 1 : 175-180.
1951. Die fruchtminierenden Arten der Gattung *Nepticula* Heyd. (*Etainia* Beirne) an der vier deutschen Ahornarten (Lep. Nept.). *Z. wien. ent. Ges.* 36 : 170-178, Taf. 14-16.
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1951. Für das Gebiet der Niederweser 1950 neu aufgefundene Microlepidopteren. *Bombus* 64/65 : 276, Nr. 500.
1951. *Pseudophia lunaris* Schff. (Lepid. Noct.). *Bombus* 66/67 : 284, Nr. 519.
1951. Zur Verbreitung von *Pachetra fulminea* F. *Bombus* 66/67 : 284-285, Nr. 520.
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1952. 1. *Zanclognatha tarsicrinalis* Knoch., 2. *Herminia derivalis* Hb., 3. *Hypenodes costaestrigalis* Stph. *Bombus* 74/75 : 316-317.
1953. *Catoptria (Semasia) heringiana* n.sp. (Eucosmidae). *Z. Lepid.* 3 : 43-45, 1 Abb..
1953. Buchbesprechung : HERING, E. Martin : Biology of the Leaf Miners, 420 pp., 2 Tfln, 180 Textabb. *Z. Lepid.* 3 : 63-64.
1953. *Aetetis (Elaphria) selini* Bsd. (Lep. Noct.) bei Bremen. *Bombus* 76/77 : 322, Nr. 617.
1953. Drei hervorragende Kleinschmetterlinge in Nordwestdeutschlands : 1. *Dioryctria faecella* Z., 2 *Myelois neophanes* Durr., 3. *Laspeyresia juniperana* Mill. *Bombus* 76/77 : 323- 324, Nr. 621.
1953. *Polyploca ridens* F. wiederfunden. *Bombus* 78/79 : 333, Nr. 631b.
1955. Schutzvorrichtung zum Bau des Verpuppungskokons bei Arten der Gat-

tung *Bucculatrix* Z. und *Lyonetia* Hb. *Z. wien. ent. Ges.* 40 : 118-121, Taf. 6-9, Nachtrag : 40 : 206.

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1956. *Tubuliferodes josephinae* Toll in Nordwestdeustchland. *Bombus* 95/96 : 402, Nr. 719.

1957. Eine weitere in Deutschland an *Aster linosyris* (L.) Bernh. lebende *Coleophora*-Art. *Dt. ent. Z.* 4 : 54-60.

1957. Auffällig häufiges Auftreten des Totenkopfes, *Acherontia atropos* L. 1956 im Niederwesergebiet. *Bombus* 97/98 : 410, Nr. 726.

1958. *Hipparchia statilinus* Hufn. bei Pevesdorf an der Elbe, Kreis Lüchow. *Bombus* 2 : 10-11, Nr. 15.

1958. *Polia glauca* Hb. im Lande Oldenburg : *Bombus* 2 : 40, Nr. 47.

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1960. Eine neue Art aus der Gattung *Pseudeucosma* Obr., *Pseudeucosma subtilana* nova species. *Boll. Zool. agr. Bachic.*, Serie II : 127-135.

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Nota lepid. 17 (1/2) : 100-104 ; 30.XI.1994 ISSN 0342-7536

Book reviews — Buchbesprechungen — Analyses

Coleophoridae dell'Area Irano-Anatolica e regioni limitrofe (Lepidoptera). Contribuzioni alla conoscenza dei Coleophoridae. LXXV. Giorgio Baldizzone. 423 pp., 698 photos b/n. Associazione Naturalistica Piemontese, Memorie, III. En vente exclusivement chez Apollo Books, Kirkeby Sand 19, DK-5771 Stenstrup, Danemark, DKK 390, frais d'expédition exclus. Présentation par le Prof. Emilio Balletto, Président de la Societas Europaea Lepidopterologica.

Vient de paraître le troisième volume des «Memorie» de l'«Associazione Naturalistica Piemontese», qui depuis quelques années publie aussi un intéressant Bulletin dédié surtout à l'histoire naturelle subalpine. Ce volume des «Memorie» est monographique et comprend seulement le travail de Giorgio Baldizzone relatif aux Coleophorides de la zone Irano-Anatolienne et des régions limitrophes. Après l'importante révision des Coleophorides chinois, de l'Inde, de l'Australie et de l'Afrique tropicale, Baldizzone nous présente aujourd'hui en détail la faune du Proche- et Moyen-Orient. Ce travail représente sa 75^e contribution à la connaissance de cette vaste et complexe famille des Microlépidoptères Gelechioidea, dont il est depuis longtemps un spécialiste reconnu.

Comme le rappelle dans sa préface Emilio Balletto, Président de la «Societas Europaea Lepidopterologica», la région irano-anatolienne est très peu connue, non seulement en ce qui concerne les microlépidoptères ; le travail de Baldizzone doit donc être particulièrement apprecié pour l'évidente et vaste contribution qu'il apporte au progrès des connaissances relatives à la faune des Lépidoptères de cette importante zone de la Région Paléarctique. Dans cette monographie, dédiée à la mémoire de Eberhard Jäckh récemment disparu, sont traités 310 taxa appartenant aux Coleophorides, dont 84 sont ici décrits pour la première fois sur la base d'un large matériel provenant en majorité des campagnes de recherche de microlépidoptéristes connus, parmi lesquels les plus importants sont sans doute Fritz Kasy, Wolfgang Glaser, Hans Georg Amsel et Eva Vartian. Les nouveaux taxa appartiennent tous au genre *Coleophora*, sauf une espèce du genre *Ischnophanes*. L'auteur a en outre fixé 30 lectotypes et le néotype de *C. gypsophilae* Christoph, 1862 (= *C. vicinella* Zeller, 1849). Enfin sept nouvelles synonymies sont reconnues ; ces dernières, ajoutées aux nombreuses déjà signalées par Baldizzone lui-même ou par d'autres auteurs, permettent de compléter la révision nomenclatoriale des taxa paléarctiques.

Comme d'habitude, la très abondante iconographie qui accompagne le travail est très claire et parfaite sur le plan technique, soit en ce qui concerne l'habitus des adultes — il est dommage que les hauts frais d'impression ne permettent pas de les reproduire en couleur comme on l'a fait sur la couverture avec la splendide planche du jeune entomologiste Fabrizio Pensati! — soit en ce qui concerne les genitalia des deux sexes.

Ce travail, d'après une indication très claire de son auteur, veut seulement mettre à jour la connaissance des Coleophorides de la région irano-anatolienne au sens large, en renvoyant à des contributions ultérieures la révision moderne de la systématique du groupe et toute autre considération zoogéographique. Dans sa contribution en effet, Baldizzone maintient pour l'instant la subdivision classique donnée par Toll, qui divise les Coleophorides en plusieurs groupes pas nécessairement naturels, reconnus sur la base des plans de structure des genitalia des deux sexes. En lisant avec attention la monographie, on peut de toute façon dejà obtenir plusieurs indications zoogéographiques tout à fait intéressantes qui nous permettent de confirmer ou de mieux comprendre le peuplement des régions anatoliennes, arabes et du bassin touranique.

De toute façon, ce volume, à tirage limité à 400 copies à cause des frais d'impression élevés auxquels l'auteur a dû faire face lui-même pour la plupart, est non seulement à conseiller vivement à tous ceux qui étudient les Lépidoptères, mais aussi à tous ceux qui désirent augmenter leurs connaissances en matière d'entomologie et de zoogéographie.

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Index of economically important Lepidoptera. Bin-Cheng Zhang, 1994. 599 Seiten, gebunden. CAB International, Wallingford, Oxon, UK. ISBN 0-85198-903-9. £ 50 ohne, £ 70 mit Diskette.

Das Commonwealth Agricultural Bureau International (CABI), wurde 1928 gegründet. Eine der wesentlichen Aufgaben des CAB's ist die Herausgabe von Referateorganen über die Weltliteratur im Agrarbereich im weitesten Sinne. Unter anderem erscheint das "Review of Agricultural Entomology" (RAE) (früher: "Review of applied Entomology") 1994 bereits im Volume 82 und zwar gegründet 1913, also schon vor der Etablierung des CABI. Da jährlich ca. 10.000 Arbeiten referiert werden, hat sich im Laufe der Jahre natürlich ein enormer Datenbestand angesammelt. Verständlich, daß dieser riesige Fundus nach zusätzlichen 'Ertragsmöglichkeiten' durchforscht wird. Begrüßenswert für die 'User' der Reviews, wenn ihnen das geballte Wissen, praxisgerecht serviert wird. Praxisgerecht bedeutet in diesem Falle, daß Herr Zhang aus dem RAE-Datenbestand, alle Lepidopteren herausselektiert hat, die seit 1913 in der Literatur eine Erwähnung als 'Pflanzenschädlinge' fanden. Parasiten des Menschen und der Tiere sollen separat behandelt werde. Eine derartige Kompilation bedeutet für jeden angewandten Entomologen eine sehr große Hilfe. Dafür sei Herrn Zhang und dem CABI Dank. Schließlich hat nicht jeder die technischen Einrichtungen und die finanziellen Möglichkeiten, die leider sehr teure elektronische Datenbank des CABI zu benutzen.

Allerdings möchte ich einige 'Schwachstellen' auflisten, die ich gerne bei einer Neuauflage beseitigt sehen würde.

Daß bei der großen Datenfülle auch mal etwas verloren geht, dürfte verständlich sein. Einige wenige Arten habe ich vermißt, so zum Beispiel *Duponchelia fovealis* (in RAE 1991 ; no. 743, 5542 und 6335). Die Angaben zur geographischen Verbreitung sind immer mit Vorsicht zu handhaben, da viele Länder nicht sehr meldefreudig sind. Allerdings hat Herr Zhang auch nicht alle Angaben aus den Reviews übernommen, so zum Beispiel bei *Opogona sacchari.* Ein besonderes Problem sind die Wirtspflanzenangaben. Wenn bei *Epichoristodes acerbella* nur drei Wirtspflanzen genannt sind, so ist mir dies unverständlich. Die Larve dieses Tortriciden ist zweifellos polyphag und man könnte ohne weiteres 20 bis 30 Wirtspflanzen nennen bzw. der Literatur entnehmen. Beim European corn borer *Ostrinia nubilalis* hätte er etwa 300 Pflanzenarten aufführen können. Aus Platzgründen (oder auch aus Zeitgründen ?) wurde wohl selektiert. Wäre es, in diesem wie in ähnlichen Fällen, nicht besser gewesen, wirklich nur die Hauptwirtspflanze(n) anzugeben und dann auf die Polyphagie zu verweisen ? Personen, die diese Lepidopteren nicht näher kennen, könnten sonst solche unvollständige Auflistungen für bare Münze nehmen. Die Vermischung der 'common names' mit den wissenschaftlichen Namen in den Host Records dient auch nicht gerade der besseren Übersicht.

Etwas ganz wichtiges für den angewandten Entomologen fehlt jedoch total : ein Wirtspflanzenindex. Es wäre wirklich sehr hilfreich, einen Überblick zu bekommen, welche Lepidopteren an welchen Pflanzen vorkommen können. Da das Buch weitgehend mit Hilfe der EDV geschrieben wurde, dürfte die Erstellung einer derartigen Liste kein Problem darstellen. Der 'Index of specific and infraspecific epithets' am Schluß des Buches ist zwar sehr umfangreich, wäre aber mit Seitenangaben besser brauchbar. Vermutlich aus Platzgründen wurde bei den Hinweisen zu den RAE References nur die Bandzahl genannt. Die zusätzliche Angabe der Abstract-Nummer wäre sehr hilfreich und würde das Buch meines Erachtens kaum umfangreicher machen.

Insgesamt gesehen, stellt das Buch jedoch auf Grund der ungeheuren Datenfülle eine äußerst wertvolle Arbeitsgrundlage für alle Biologen, Ökologen und natürlich speziell für Entomologen dar und ist für Entomologen im Bereich Pflanzenschutz eigentlich unverzichtbar. Es wäre sehr zu wünschen, wenn weitere derartige Indexe auch für andere Insektenordnungen erscheinen würden.

Wolfgang Billen

Guide pour l'identification des espèces françaises du genre Zygaena. Louis Faillie, 1994. 52 pages, 56 figures au trait, 3 planches couleur hors texte. Format 14,8 x 21 cm. Édition J-M Desse. Prix 90 FFr plus port. En vente chez l'auteur ; 8 rue Polonaise F-72200 La Flèche.

Ce guide publié à compte d'auteur le 19-III-1994 est destiné à permettre l'identification rapide et sûre de toutes les espèces du genre *Zygaena* actuellement connues en France. L. Faillie aurait donc pu se contenter de la partie centrale du guide, nous en aurions disposé déja depuis plusieurs années. Ce perfectionniste ne pouvait se contenter de cet à peu près. Il a donc cherché à mettre en perspective l'objet du guide. Celui-ci débute par quelques considérations sur les notions biologiques qui conduisent à la systématique bien documentée permettant d'approcher la finesse de la pensée des grands spécialistes contemporains qui guident l'étude de ce groupe d'espéces.

Elles illustrent aussi le bon sens qui privilégie les solutions simples aux considérations trop théoriques ou partielles qui ont souvent obscurci l'horizon des études se rapportant à ce groupe.

Suit la liste des espèces du genre *Zygaena*, tirée de la solution proposée par C. M. Naumann & W. G. Tremewan en 1984, suivie de rappels au sujet de la position de Zygaenidae fossiles vis-à-vis de ce genre et des genres voisins. Les 26 espèces françaises qui sont l'objet du guide, sont ensuite énumérées dans le même ordre. Un intéressant tableau de comparaison avec les pays européens limitrophes ou voisins, permet de visualiser la richesse et la variété des espèces de chacun d'eux.

Dans les 18 pages suivantes le lecteur trouvera les traits essentiels d'une diagnose de chacune des espèces françaises qui décrit parfaitement les caractères distinctifs externes, complétés par un dessin au trait grandeur nature qui met l'accent sur les parties de l'ornementation alaire ou du corps qu'il faut prendre en compte pour déterminer chaque espèce. Ces caractères sont souvent mis en évidence par une flèche qui attire judicieusement l'attention du lecteur.

Pour les espèces présentant une variation importante, L. Faillie n'a pas hésité à réaliser plusieurs dessins qui illustrent les principales sous-espèces ou morphes présentes en France. Il y a ajouté souvent des informations très pertinentes et très à jour sur la répartition, la génétique, la nomenclature ou la taxinomie. Cette partie centrale du guide permet vraiment de réaliser les déterminations correctes dans la plupart des cas. Les pièges et difficultés essentielles sont d'ailleurs révélés afin de permettre à tous de travailler avec un maximum de sécurité.

Le guide est complété par un tryptique amovible regroupant sur trois planches photographiques en couleur, les 72 specimens représentant au moins une fois, grandeur nature, chacune des 26 epèces traitées. Cette disposition permet, lors de la détermination, de comparer le dessin au trait avec la figure en couleur et renforce ainsi la qualité de la détermination. Il convient de saluer le soin apporté au choix des exemplaires reproduits, car ils sont tous en parfait état de fraîcheur et correctement préparés, ce qui est rare dans les publications concernant ce groupe.

Pour augmenter l'efficacité des déterminations, l'auteur a ensuite judicieusement regroupé les espèces suivant certains critères ornementaux (anneau abdominal et collerette) puis regroupé à la fin du guide, sur 4 pages, tous les dessins au trait représentant les imagos figurant dans la partie centrale. Quelques considérations sur la structure interne des genitalia mâle des *Zygaena* sont ensuite les bienvenues. Elles permettent de bien comprendre les différences entre *Z. minos* et *Z. purpuralis* dont la dissection est obligatoire.

Une bibliographie adaptée au guide permettra enfin au lecteur d'approfondir les connaissances qu'il aura acquises à la lecture du guide.

En résumé, un petit livre intelligent, fruit de décennies d'études dédiées aux zygènes et de rencontres avec les plus grands spécialistes de la question. Marque aussi d'une volonté de se mettre au service des autres pour les aider à comprendre. Remercions donc chaleureusement Louis Faillie d'avoir consacré beaucoup de son temps à la réalisation de ce petit fascicule qu'il a tenu à financer de ses propres deniers afin de ne dépendre d'aucune obédience.

Faisons bon accueil à ce guide qui, je n'en doute pas, deviendra très vite le compagnon indispensable de vos recherches et de vos promenades à la rencontre des zygènes.

Eric DROUET

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Editorial

The Editor would like to apologise for the late publication of this issue. This has been due to illness in the Editor's family, on top of increased professional and private commitments during February and March. For the same reason, the SEL "1991-1992 Index of Publications on European Lepidoptera" was also delayed. The situation is again under control and all outstanding correspondence will be dealt with as soon as possible.

I am pleased to announce that Dr. Roger Dennis, Wilmslow, GB has joined the Editorial Committee of this Journal. Dr. Dennis, who is well known for his articles and books on ecological lepidopterology, has already been a great help in the processing of a number of manuscripts in English. Such manuscripts from the United Kingdom may now be submitted directly to Dr. Dennis. In addition, M. Yves Gonseth, Neuchâtel, Switzerland has agreed to act as Assistant Editor from June 1995. At the same time, Dr. Hansjürg Geiger will leave us. Dr. Geiger has been an invaluable member of the Editorial Committee since 1986, but wishes to step down due to increased professional commitments. I would like to sincerely thank Dr. Geiger, not only for his editorial contribution, but also for his advice and moral support.

Finally, I would like to mention that this Journal is now abstracted in BIOSIS and "Current Advances in Ecological and Environmental Sciences", a CABS review journal.

Steven WHITEBREAD

Nota lepid. 17 (3/4) : 107-112 ; 30.IV.1995 ISSN 0342-7536

Anumeta arax sp. n. from Turkish Armenia (Lepidoptera, Noctuidae, Catocalinae)

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Summary

During a lepidopterological visit to Turkish Armenia in 1989 a new species of *Anumeta* Walker, 1858. was found. This is described here as *Anumeta arax* sp. n. In September 1993 a further visit to this area was made. A few notes on collecting in this politically very tense, but entomologically very interesting area are given.

Résumé

Découverte d'une nouvelle espèce d'*Anumeta* Walker, 1858 au cours d'une expédition lépidoptérologique en Arménie turque en 1989. Description de celle-ci sous le nom d'*Anumeta arax* sp. n. L'auteur a revisité ces lieux en septembre 1993 et donne quelques indications sur la chasse aux papillons dans cette région, où la situation politique est très tendue, mais qui est très intéressante pour les entomologistes.

Introduction

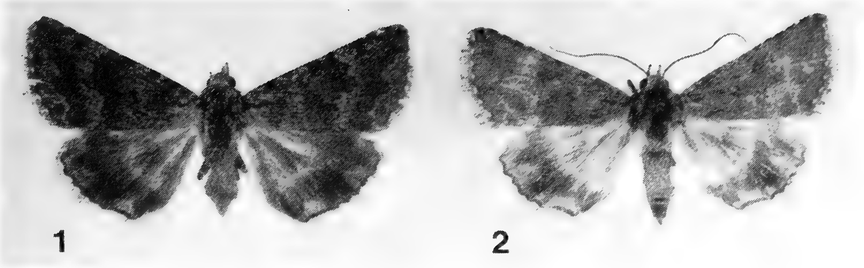
Turkish Armenia is one of the most beautiful and lepidopterologically important areas in the western Palaearctic region. However, since 1988 it has not been fully safe to travel, camp or catch insects because of the unstable political situation in the area. The Arax valley is perhaps the most interesting locality of the region. It runs east-west at a low level (at Aralik : 825 m) just north of, and below, the imposing Mt. Ararat. Unfortunately, the Turkish, Armenian and Kurdish peoples all claim sovereignty over the area, which is at present situated in Turkey. By the end of 1993, the tense situation had become distinctly dangerous for touring lepidopterists who wanted to collect in the area. Together with the Danish lepidopterist, Fritz Schepler, I visited the area at the beginning of September 1993. We collected at night only with "black" lamps (pure ultraviolet 125 watt bulbs and 20 watt tubes), and were as usual met by the very friendly local people, but also by masses of heavily armed, friendly gendarmes and soldiers. Everybody was scared of each other, often with good reason, and this anxiety creates aggression.

When I worked in the area in 1989, Nils Esser (a Danish coleopterist) and I were allowed by the gendarmes to camp and catch moths along the asphalt road from Igdir to Aralik, but we had to set up the lamps within 5 metres from the road, and we were not allowed to stay. In 1993 it was impossible — even armed with psychological arguments rehearsed in my mind — to obtain the same permission. We were forced to camp in a storm (only catching with an 8 watt superactinic tube two metres from the car) close to the military camp in the middle of the village of Hasanhan, approx. 30 km west of Aralik. The unexpected, but good records from both visits to the area will be published in a later paper. Here I will only mention the catch in 1989 of a dozen specimens of *Drasteria picta* (Christoph, 1877), two specimens of *Gonospileia munita* (Hübner, [1813]), both species new to Turkey, and in 1993 the record of two specimens of *Cardiestra vassilinini* (A. Bang-Haas, 1927), also new to Turkey and previously only known from the type specimen.

In 1989, I also captured one specimen of the genus *Anumeta* Walker, 1858 which was unknown to me and to everyone to whom I showed it. Not until 1992 in St. Petersburg, visited in connection with the successful SEL Congress in Helsinki, did I find four more specimens of "my" *Anumeta* in the Zoology Institute, Russian Academy of Science. They were placed under the name *caucasica* Rjabov, in litt. Dr. Irina L. Sukhareva who kindly helped me during my visit also translated the Cyrillic writing on the labels. The four specimens were all recorded from the Armenian side of the Arax valley (former Armenian S.S.R.) within 10 km from the locality in Turkey where I found it : 10 km north west of Aralik. As the name *caucasica* to my mind should represent a mountain species further to the north, I have decided to describe it here under the name *Anumeta arax* **sp. n.**

Anumeta arax sp. n.

Holotype : ♂ (Fig. 1) Turkey, prov. Kars, 10 km NW Aralik, 825 m, 22.vii.1989, genit. prep. 1798, leg. & coll. M. Fibiger.
Paratypes : 1 ♂ [Turkey], Aralych [Aralik]. 1 ♀ [Armenia], Mtschjan Artashantski region (Arax valley), Okt., leg. Arutjunjan. 1 ♀ [Armenia], Dzhuga by Dzhulfa [Arax valley], 4.vii.1932, leg. Rjabov. 1 ♀ (Fig. 2, allo-



Figs 1-2. *Anumeta arax* sp. n. 1 — Allotype, female ; 2 — Holotype, male.

TYPE) Armenia, Burastan, Acerjan [Kamarlu region, Arax valley], at light, 26.vi.1948, leg. G. Azaryan, genit. prep. 1799 M. Fibiger.

DESCRIPTION (Figs 1,2) : Male and female similar in size and wing pattern ; female colouration in fore and hindwing slightly darker. Wingspan : 33-34 mm. All segments of labial palpi porrect ; first segment light grey, as long as second and third together, latter two black. Antenna of male ciliate, of female filiform. Ground colour of head, thorax and forewing blackish grey. Basal and median area of forewing slightly darker. Black costal spots on and between crosslines. Lines weakly defined except for black terminal line on both wings, which is sinuate with white spots between veins on terminal side. Forewing fringes dark grey, whitish on hindwing. Stigmata absent, a black spot near reniform. Hindwing with light greyish median band, terminal area darker than basal. Whitish blotches on termen of hindwing (typical for *Anumeta* and *Drasteria*) weakly defined in male, hardly visible in female. Underside light greyish powdered with black scales. Terminal area blackish. Median stigma present on hindwing.

MALE GENITALIA (Fig. 3) : Valva, juxta, and vinculum rather simple, but uncus prominent, heavily sclerotised, with apical hook. Aedeagus straight, no cornutus, but a light sclerotised band. Vesica short, rounded with small diverticula.

Note : The preparation of the vesica was not perfect and the paratype male had already been dissected, so it was not possible to evert.

FEMALE GENITALIA (Fig. 4) : Ovipositor hairy. Apophyses equally broad their whole length. Eighth segment hairy distally. Ductus bursa weakly sclerotised. Corpus bursa unisaccate, cylindrical, two and a half times as long as broad.

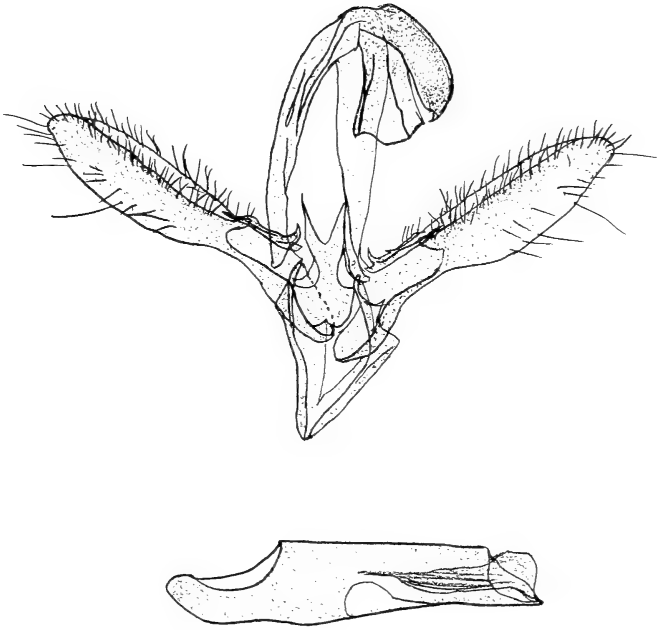


Fig. 3. Male genitalia of *Anumeta arax* sp. n. : holotype.

Remarks

Because of an urgent need for a revision of the genus *Anumeta*, which also forms the tribe Anumetini, the exact number of species cannot be stated. A little more than a score of *Anumeta* species are known, all with a desert and semi-desert, central and southwestern Palaearctic distribution. Only three species are recorded from Europe (Fibiger & Hacker, 1991), in south-east European Russia. The genus was previously unknown from Turkey.

Systematically, *Anumeta arax* sp. n. is most closest related to *Anumeta fricta* (Christoph, 1893), *A. fractistrigata* (Alphéraky, 1882) and *A. cestina* (Staudinger, 1884).

The name of this new species is derived from the type locality : The Arax valley.

Fig. 4. Female genitalia of *Anumeta arax* sp. n. : allotype.

Acknowledgements

Dr. Irina L. Sukhareva is sincerely thanked for her assistance in the Zoological Institute, St. Petersburg. My wife Mariann and Barry Goater are as usual thanked for checking my English.

Literature

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Nota lepid. 17 (3/4) : 113-119 ; 30.IV.1995 ISSN 0342-7536

Redescription of *Elachista differens* Parenti, 1978 (Lepidoptera, Elachistidae)

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Summary

Elachista differens Parenti is redescribed and compared with the other recognized West-Palaearctic species of the *Elachista gleichenella* group on the basis of a series collected in Rhineland, Germany. The female is described for the first time. The species externally closely resembles *E. gleichenella* (Fabricius) and *E. lambeseella* Nielsen & Traugott-Olsen. The structure of male genitalia indicates *E. lambeseella* to be the closest relative of the species. *E. differens* is also reported from Corfu, Greece, although the male genitalia show some minor differences.

Zusammenfassung

Elachista differens Parenti, 1978, wird erneut beschrieben und ausserdem verglichen mit den anderen bekannten westpalearktischen Arten der *Elachista gleichenella*-Gruppe auf der Grundlage einiger im Rheinland, Deutschland, gefundenen Faltern dieser Art. Das bisher unbekannte Weibchen wird zum ersten Mal beschrieben. Die Art gleicht äusserlich sehr der *E. gleichenella* (Fabricius) und *E. lambeseella* Nielsen & Traugott-Olsen. Der Bau der männlichen Genitalien zeigt, dass *E. lambeseella* am nächsten verwandt ist mit dieser Art. *E. differens* wird ebenfalls nachgewiesen von Korfu, Griechenland, obgleich die männlichen Genitalien der dort gefundenen Tiere einige kleine Abweichungen zeigen.

Résumé

Redescription d'*Elachista differens* Parenti et comparaison de celle-ci avec d'autres espèces ouest-paléarctiques connues du groupe d'*Elachista gleichenella* en se basant sur quelques exemplaires trouvés en Rhénanie (Allemagne). Description de la femelle, jusqu'à présent encore inconnue. Extérieurement, *E. differens* ressemble beaucoup à *E. gleichenella* (Fabricius) et à *E. lambeseella* Nielsen & Traugott-Olsen. La structure des genitalia mâles montre que cette espèce est la plus proche de *E. lambeseella*. Elle a aussi été signalée de Corfou, Grèce ; les genitalia mâles des exemplaires de ces deux régions présentent toutefois quelques petites différences.

Introduction

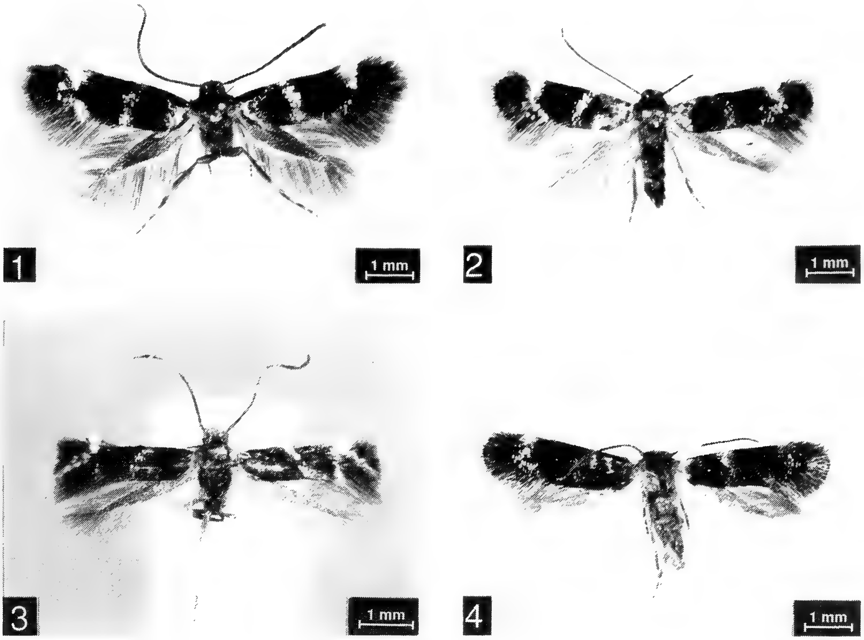
In the Palaearctic region five *Elachista* species belonging to the *gleichenella* group sensu TRAUGOTT-OLSEN and NIELSEN (1977) have so far been described : *E. gleichenella* (Fabricius, 1781), *E. regificella* Sircom, 1849, *E. differens* Parenti, 1978, *E. lambeseella* Nielsen & Traugott-Olsen, 1987 and the eastern Palaearctic *E. megagnathos* Sruoga, 1990. The description of *E. differens* was based on three male specimens collected from France (type locality) and Italy. The original description (PARENTI, 1978) contained only a short description of the external characters and a schematic figure of the male genitalia ; NIELSEN & TRAUGOTT-OLSEN (1987) therefore ignored this species when describing *E. lambeseella* (type locality Algeria, Lambése), even though these species are closely related. Additional material has shown that *E. differens* is rather widespread in Europe. In this paper we give a redescription of this species, including a description of the previously unknown female.

Elachista differens Parenti, 1978

MATERIAL STUDIED : D NW-Nordeifel Marmagen, Gillesbachtal, 4.7.1992 1 ♀, 8.7.1992 1 ♂ 1 ♀, 3.7.1993 4 ♂♂ 6 ♀♀, 4.7.1993 5 ♀♀ Biesenbaum leg. Coll. Zoological Museum, University of Helsinki (2 ♂ 2 ♀), and coll. Biesenbaum. Greece, Corfu, 6.-14.6.1978, Vesa Varis leg., 8 ♂♂ in Coll. Zoological Museum, University of Helsinki.

DIAGNOSIS : Externally *Elachista differens* resembles *E. gleichenella* (Fabricius), but it is on average larger. Costal and tornal spots are usually separated in *E. differens*, whereas they almost always are joined in *E. gleichenella*, forming a fascia (Figs 1-2, 4). These species are readily distinguished by the very different shape of valva, uncus lobes and aedeagus in the male genitalia (Figs 5 and 7). In the female genitalia the diagnostic characters of *E. differens* are the non-sclerotized antrum and colliculum, narrower signum and pyriform corpus bursae (Figs 11-12, 14). The colliculum of *E. gleichenella* is dorsally sclerotized (Fig. 15) ; the corpus bursae is constricted just below middle (Fig. 13) [this character is ignored in TRAUGOTT-OLSEN & NIELSEN (1977 : Fig. 401]).

The male genitalia of *E. differens* somewhat resemble those of *E. regificella* Sircom, but the gnathos is much larger, and the aedeagus



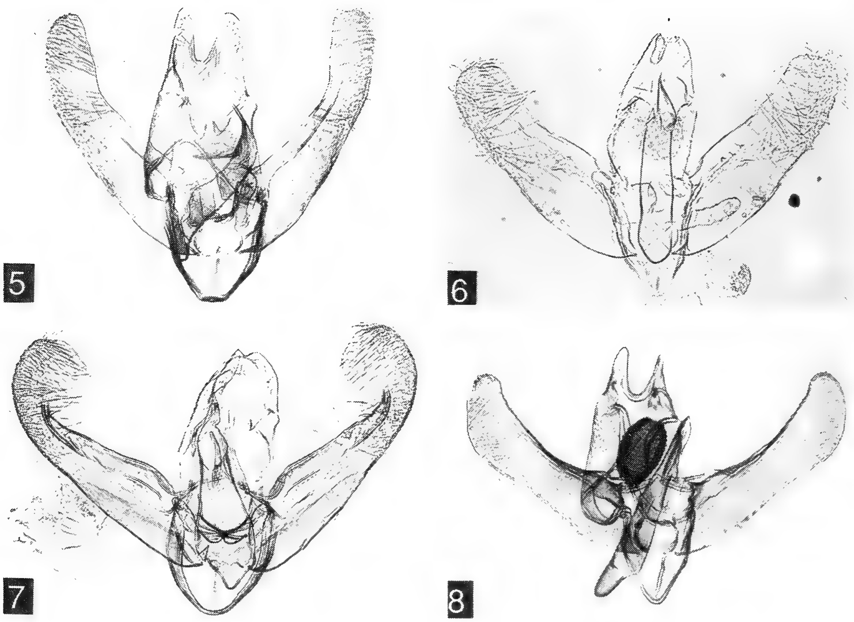
Figs 1-4. Habitus of *Elachista* spp. : 1 — *E. differens* Parenti ♂ (Nordeifel, Germany) ; 2 — *E. differens* ♀ (Nordeifel, Germany) ; 3 — Holotype ♂ of *E. lambeseella* Nielsen & Traugott-Olsen (Lambése, Algeria) ; 4 — *E. gleichenella* (Fabricius) ♀ (S. Germany).

is straight in *E. regificella* (Fig. 8). The female of *E. regificella* has a longitudinal, dentate sclerotization in the colliculum (Fig. 16), which is lacking in *E. differens*.

Based on male genitalic characters *E. lambeseella* Nielsen & Traugott-Olsen, 1987 seems to be the closest relative of *E. differens*. Externally *E. differens* can be separated from this species by the broader forewing and larger size (Figs 1-3). In the male genitalia the uncus lobes are longer and more slender, the valva is narrower, the cucullus of the valva is more elongate and slightly bent and no cornuti are present in the aedeagus (Figs 5-6, 9-10). The female of *E. lambeseella* remains unknown.

Redescription
(Figs 1-2, 5, 9-10, 11-12, 14)

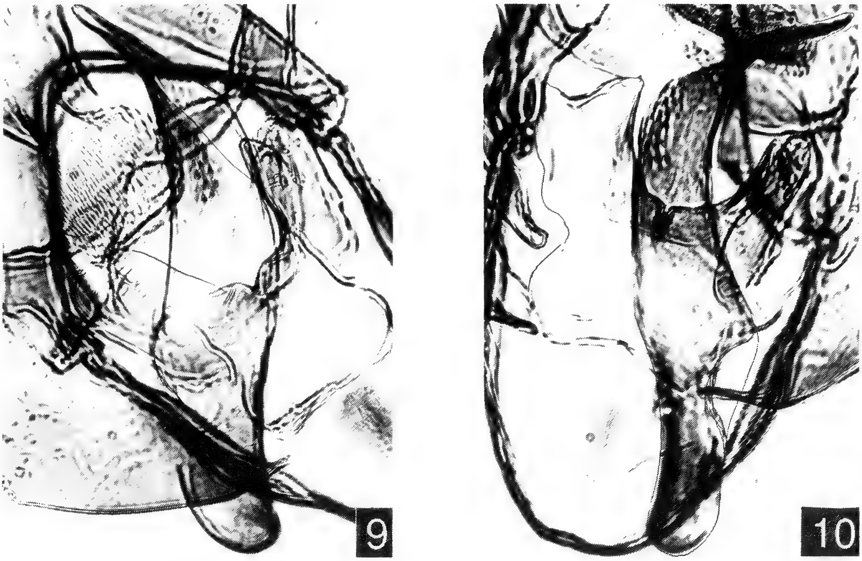
Labial palpi drooping, slightly curved, leaden grey, third segment slightly shorter than second. Head and neck tufts leaden grey with



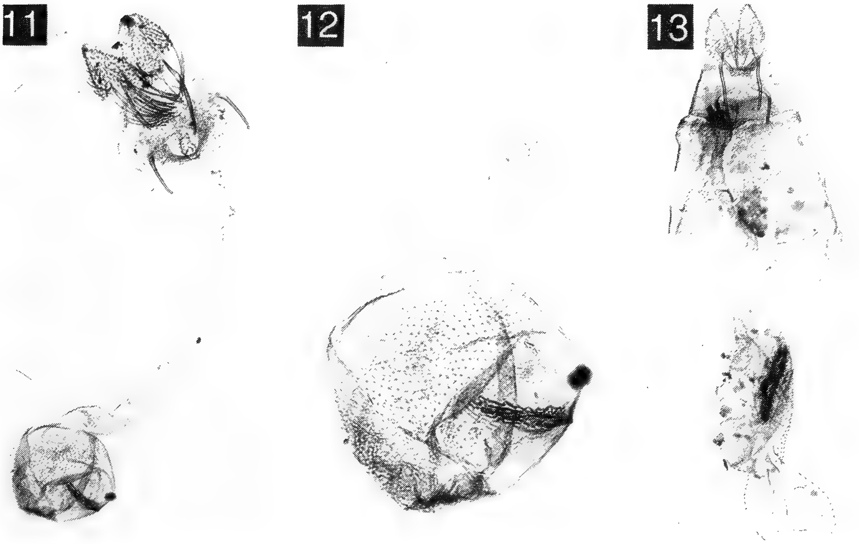
Figs 5-8. Male genitalia of *Elachista* spp. : 5 — *E. differens* Parenti (L. Kaila prep. no. 1136) ; 6 — Holotype of *E. lambeseella* Nielsen & Traugott-Olsen (prep. E. S. Nielsen 1776) ; 7 — *E. gleichenella* (L. Kaila prep. no. 444) ; 8 — *E. regificella* (L. Kaila prep. no. 1127).

metallic sheen. Antennae unicolorous grey, in distal 2/3rds segments with distally slightly raised scales. Tegulae, thorax and abdomen leaden grey with metallic sheen. Legs grey, underside of tibia creamy white, tarsal segments with white distal rings. Forewing ground colour mottled black with bronzy sheen ; base shining silvery ; fascia from before middle of costa to middle of dorsum, silvery with bluish or greenish reflection ; triangular costal spot creamy white at costa, towards middle of wing silvery just beyond opposite silvery tornal spot ; an irregular third spot between tornal spot and apex formed by some silvery scales ; especially in female the three spots often joined forming fascia with medial angle towards apex. Hindwing and underside of wings grey. Forewing length 3.5-4 mm in male (n = 4), 2.5-4 mm in female (n = 13). Most female specimens smaller than males.

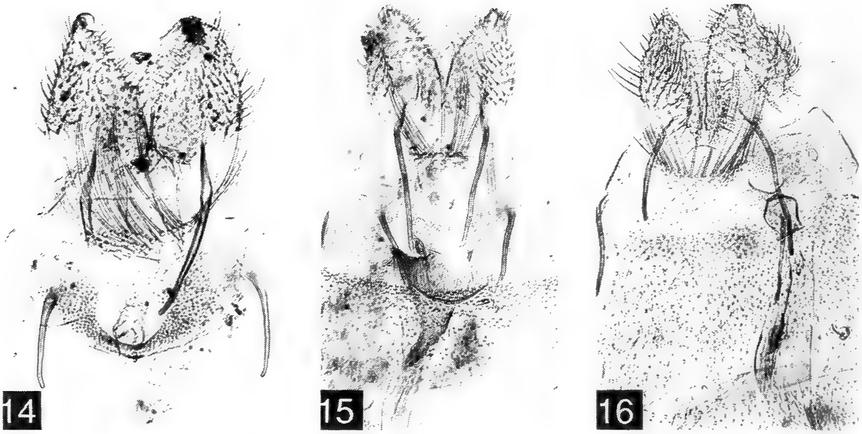
MALE GENITALIA : Uncus lobes long, gradually tapering toward rounded tip, with row of stout setae. Gnathos large, rounded. Valva rather narrow, tapering towards tip ; costa straight, well sclerotized ; cucullus



Figs 9-10. Male genitalia of *E. differens* : 9 — aedeagus with carina in the margin of distal opening (L. Kaila prep. no. 1133) ; 10 — juxta lobes (L. Kaila prep. no. 1134).



Figs 11-13. Female genitalia of *Elachista* spp. : 11, 12 — *E. differens* (L. Kaila prep. no. 1137) ; 13 — *E. gleichenella* (L. Kaila prep. no. 1132).



Figs 14-16. Region of ostium bursae in female genitalia of *Elachista* spp. : 14 — *E. differens* (L. Kaila prep. no. 1137) ; 15 — *E. gleichenella* (L. Kaila prep. no. 1131) ; 16 — *E. regificella* (L. Kaila prep. no. 1130).

elongate with rounded tip, slightly bent forming an angle with costa. Digitate process rather broad, blunt, with setae. Juxta lobes separated by short incision medially, almost parallel-sided, truncate, apical margin slightly rounded near the incision ; with short, pointed lateral process. Vinculum rounded, with indistinct median ridge. Aedeagus short and broad, S-shaped ; caecum processed, blunt ; distal part oblique, tapering into strongly pointed distal end, margin of distal opening laterally asymmetrical with elongate carina ; without cornuti.

FEMALE GENITALIA : Distal margin of eighth tergite with long setae. Apophyses stout, posteriores three times longer than anteriores. Ostium bursae rounded with strongly sclerotized margins. Antrum very short, funnel-shaped, neither antrum nor colliculum sclerotized. Corpus bursae rounded with small internal spines ; signum elongate, dentate.

Remarks

We consider the series from Greece, Corfu, to belong to *E. differens*, although the uncus lobes seem to be slightly narrower, and carina of aedeagus is smaller in these specimens. These differences are in our opinion minor, and the material available does not allow taxonomic separation of these populations. Further material is needed for an evaluation of the geographic variation of the species.

Acknowledgements

B. Krutzsch (Berlin) loaned us the holotype of *Elachista lambeseella.* R. Tyynelä helped with photographs, and K. Mikkola made valuable comments on the manuscript. We thank all these persons for their help.

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Dr. h.c. Karl Burmann †

Wir haben die traurige Pflicht Ihnen
mitzuteilen, dass der bekannte
oesterreichische Lepidopterologe
Dr.h.c. Karl Burmann tot ist.
Er starb am 26. März 1995
im 87. Lebensjahr.

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Aricia crassipuncta bassoni Larsen, 1974 from Lebanon raised to species rank (Lepidoptera, Lycaenidae)

Torben B. LARSEN

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Summary

A reexamination of material of *Aricia crassipuncta bassoni* Larsen, 1974 from Lebanon shows that it differs from *A. vandarbani* Pfeiffer, 1937 from Iran, with which it had been synonymised, and also from *A. anteros* Freyer, 1838 [Turkey] and *A. crassipuncta* Christoph, 1893 [Armenia]. The differences are to be found in wing pattern and shape, and in the male genitalia. The taxon is therefore raised to species rank.

Résumé

Le réexamen de matériel d'*Aricia crassipuncta bassoni* Larsen, 1974 du Liban, montre qu'il diffère de *A. vandarbani* Pfeiffer, 1937 d'Iran, avec lequel il avait été synonymisé, et également d'*A. anteros* Freyer, 1838 (Turquie) et d'*A. crassipuncta* Christoph, 1893 (Arménie). Les différences sont à trouver dans les dessins et les formes des ailes, ainsi que dans les genitalia mâles. Le taxon est en conséquence élevé au rang d'espèce.

In 1974, I described the taxon *Aricia crassipuncta bassoni* from the high mountains of Lebanon. It belongs in the subgenus *Ultraaricia* Beuret, 1959, a small group of species characterized by the presence of an unusual inferior lobe in the uncus. On the advice of Dr. Burkhardt Alberti and Dr. Walther Forster, I allied the Lebanese taxon with *A. crassipuncta* Christoph, 1893 from Armenia, despite their being separated by a distance of more than a thousand kilometres. I was encouraged to do this also because the Lebanese population was traditionally referred to tentatively as ssp. *crassipuncta* of *Aricia anteros* Freyer, 1838.

In a paper in this journal, NEKRUTENKO (1980) placed the taxon *bassoni* as a synonym of *A. vandarbani* Pfeiffer, 1937 from the Iranian Elburs Mountains on morphological grounds, though he also said it might possibly be a valid subspecies thereof. K. Schurian (pers. comm.), to

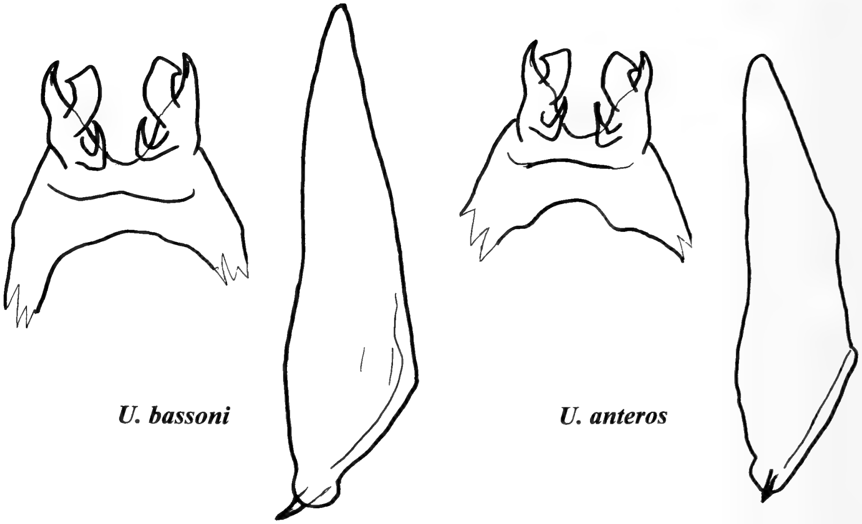

Fig. 1. Uncus and valves of *Ultraaricia* spp. : *U. bassoni* from Lebanon (Larsen prep. LAI) ; *U. anteros* from Anatolia (Ankara area) (Larsen prep. LAJ).

whom I gave some specimens, did not agree with this decision, and I had for long wanted to re-examine the issue.

After many years, I recently regained access to my genitalia mounts from Lebanon. Examination of a male *bassoni* shows that the specialized inferior lobe of the uncus is exactly like that of a male *A. anteros* from near Ankara (Fig. 1). Since the main characteristic of *A. vandarbani* is a strong reduction of this lobe, the assignment of *bassoni* to *A. vandarbani* clearly becomes impossible (no material of *bassoni* was available to Nekrutenko).

On the other hand, Nekrutenko's redescription of *A. crassipuncta*, a poorly known species, makes it clear that it differs more from *bassoni* than I thought in 1974. *A. crassipuncta* has very pointed forewings, the underside pattern is less strongly developed, the wings almost wholly lack orange marginal lunules, and the overlay of light scales is blueish-grey rather than greenish. To this must now be added that the valve of *bassoni* is proportionately longer than in the other three species, and the distal spine is long, jutting well beyond the distal end of the valve. The length of the valve is due to elongation of the basal part, the distal half having the usual proportions. I therefore raise *Aricia* (*Ultraaricia*) *crassipuncta bassoni* Larsen, 1974 to species rank **(stat.**

n.). This also seems the most reasonable solution on biogeographical grounds.

Males of *A. bassoni* (illustrated in colour by LARSEN, 1974) are readily recognized by the grey upperside with a strong, greenish sheen, usually with well developed marginal orange lunules. They are very different from the smaller blue Anatolian males. Females are like those of *Aricia agestis* Denis & Schiffermüller, 1775 with strongly developed marginal lunules. The haploid chromosome number is n = 23 (LARSEN, 1975), which has also been found in nominate *A. anteros*, and which appears to be typical for the genus. HIGGINS (1975) quotes n = 24 for *A. agestis*, but I found Lebanese males to have n = 23.

There are also occasional records of *A. crassipuncta* from southwestern Turkey (HIGGINS, 1966 ; NEKRUTENKO, 1980). It is thus possible that a population of *A. bassoni* exists in the Taurus Mountains, with which the Lebanese butterfly fauna has many other affinities, but I have not seen material from there.

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Book reviews — Buchbesprechungen — Analyses

Oekologische Untersuchungen im Unterengadin. Schmetterlinge (Lepidoptera). W. Sauter. 137 pp., kartoniert. Ergebnisse der wissenschaftlichen Untersuchungen im Schweizerischen Nationalpark Band 12, 14. Lieferung, 1993. Bestellungen an : F. Flück-Wirth, Internationale Buchhandlung für Botanik und Naturwissenschaften, CH-9053 Teufen, Schweiz. Preis : 78 Fr.

Die vorliegende Arbeit ist Teil einer interdisziplinären, durch geplante Kraftwerksbauten, angeregten Studie im Schweizer Unterengadin. Die Schmetterlingszönosen unterhalb der Waldgrenze wurden von 1961 bis 1976 mit unterschiedlicher Methodik erfaßt und durch zusätzliches Datenmaterial bis 1990 ergänzt. Insgesamt konnten 1242 Arten nachgewiesen werden, die alle einschließlich der Fundorte aufgelistet sind. In der Schweiz im wesentlichen auf das Unterengadin beschränkte Arten werden zoogeographisch analysiert. Leider konnten hier neuere Ergebnisse über *Caryocolum oculatella* nicht mehr berücksichtigt werden.

Besonders wertvoll erscheint dem Rezensenten die ökologisch orientierte Analyse der Artenbestände im 2. Teil der Studie, die trotz aller vom Autor offen dargelegten Unzulänglichkeiten eine reichhaltige Fundgrube für ähnlich gelagerte Untersuchungen im Mitteleuropa darstellt. Basierend auf den gut dokumentierten pflanzensoziologischen Verhältnissen, sowie den bekannten Daten über Raupenfutterpflanzen wurden die Arten soweit als möglich den unterschiedlichen Vegetationstypen zugeordnet. Die Zönosezugehörigkeit der einzelnen Taxa wurde möglichst exakt vorgenommen und beinhaltet im Sinne von Schwerdtfeger (1975) mehrere Kategorien von zönoseigenen Arten bis zu Irrgästen. Besonders hohe Diversitätsraten wurden im Koelerio-Poetum xerophilae (236 Arten), im Vincetoxico-Festucetum sulcatae (166 Arten) sowie im Violo-Alnetum incanae (116 Arten) nachgewiesen werden. Die Pionierstandorte des Inn sind erwartungsgemäß artenarm, weisen aber einige wichtige Vorkommen auf wie z.b. *Merulempista cingillella* (Tamariskenzünsler).

Die Studie ist trotz des relativ hohen Preises allen ökologisch orientierten Lepidopterologen wärmstens zu empfehlen, und untermauert die Bedeutung von Schmetterlingserhebungen für Aussagen über die Wertigkeit von Lebensräumen.

Peter Huemer

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Karyology and distribution as tools in the taxonomy of Iberian *Agrodiaetus* butterflies (Lepidoptera : Lycaenidae)

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Summary

A cytotaxonomical study in the main distribution areas of *Agrodiaetus ripartii, A. fabressei, A. ainsae* and *A. fulgens* revealed differences between these species. In the species with brown males, *A. ripartii* has n = 90 with two macrochromosomes and *A. fabressei* the same chromosome number, but three large chromosomes. In the species with blue males, *A. fulgens* (considered here a true species) and *A. ainsae* have n = ca. 103 and n = 108 with two and six macrochromosomes respectively. Macrochromosomes proved to be the best genetic marker to identify the species of *Agrodiaetus* in the Iberian Peninsula. By combining karyological and morphological data we were able to construct detailed UTM maps for the four species. *A. ripartii* is found from Catalonia to the Cantabrian Mountains, in the south to the Sistema Ibérico, *A. fabressei* flies in the Sistema Ibérico and Andalusian Sierras, *A. fulgens* is a Catalonian species with a very restricted distribution range and *A. ainsae* lives in the Central and Western Pyrenees and the Cantabrian Mountains. The taxon recently described as *A. violetae* is considered a subspecies of *A. fabressei*, based on the similar chromosome morphology and number. The group seems to have evolved very quickly karyologically, but morphological and ecological differences are not so evident.

Resumen

El estudio citotaxonómico en las principales áreas de distribución de *Agrodiaetus ripartii, A. fabressei, A. ainsae* y *A. fulgens* reveló diferencias entre las especies. Las especies de machos castaños *A. ripartii* y *A. fabressei* tienen respectivamente n = 90 y dos macrocromosomas y el mismo número de cromosomas, pero con tres cromosomas grandes. En el caso de las especies de machos azules *A. fulgens* (elevada aquí a la categoría de especie) y *A. ainsae* tienen n = ca. 103 y n = 108 con dos y seis macrocromosomas respectivamente. Los macrocromosomas resultaron ser el mejor marcador genético para identificar las especies del género en la Península Ibérica. Mediante el análisis conjunto de datos cariológicos, morfológicos y de distribución (estudiada con mapas detallados en proyección UTM), obtnemos una idea clara de la taxonomía del grupo. Así *A. ripartii* se encuentra desde Cataluña hasta el Sistema Cantábrico, siempre al norte del Sistema Ibérico, *A. fabressei* vive en el Sistema Ibérico y sierras andaluzas, *A. fulgens* está restringida a unas pocas localidades catalanas y *A. ainsae* vive en los Pirineos Centrales y Occidentales y los Montes Cantábricos. La recientemente descrita *A. violetae* se considera una subespecie de *A. fabressei* por su similar número y morfología cromosómicas. El grupo parece haber evolucionado muy rápidamente desde el punto de vista cariológico, mientras que las diferencias morfológicas y ecológicas no son tan patentes.

Introduction

The taxonomy of the genus *Agrodiaetus* Hübner, [1822] is one of the most complicated among Palaeartic butterflies. The genus lives mainly in the Mediterranean and Middle East, but can also be found in Central Europe and Russia (Higgins & Hargreaves, 1983 ; Kudrna, 1986). The biology is similar in the different species of the group, the larvae use sainfoin (*Onobrychis*) as foodplants, and overwinter in this stage, feeding during the following spring on the young leaves of the plant (Schurian, 1976 ; Lepidopterologische Arbeitsgruppe der Schweiz, 1987 ; Manino *et al.*, 1987; Munguira, unpublished data). Pupation takes place at the base of the plant and adults begin to fly usually after a month. The flight period ranges from July in hotter places to August in populations living at higher altitudes.

Interest in the group lies in the controversial taxonomic position of most species. Before chromosome studies were made, morphological research attempted to provide a clear view of the systematics and taxonomy of the group. Some comprehensive reviews attempted this difficult task (Forster, 1961), but the confusion generated by this approach proved the inadequacy of the methods based solely on morphological analysis. Chromosomic studies started by de Lesse in 1952, clearly showed that morphology itself was not enough to understand relationship among the species (de Lesse, 1960a). Unfortunately these studies are not a panacea either and the species' chromosome numbers also show a complicated pattern, with very different chromosome numbers in otherwise identical taxa. This shows how hard it is to give simple answers to difficult questions in a group that is undergoing a splitting process at the moment we are studying it. For example, in Italy the taxa previously grouped under the name *Agrodiaetus ripartii* (Freyer, 1830) has been split into three different species with different chromosome numbers : *A. humedasae* Toso & Balletto, 1976 with n = 38 ; *A. galloi* Balletto & Toso, 1979 with n = 66 ; and *A. ripartii* with n = 90 (Troiano *et al.*, 1979).

Agenjo (1947) lists the Spanish species as *Plebejus (Agrodiaetus) damon* (Denis & Schiffermüller, 1775), *P. dolus* (Hübner, [1823]), *P. admetus* (Esper, 1785) and *P. ripartii.* Forster (1961) describes *ainsae* as a subspecies of *dolus* and considers *Agrodiaetus* as an independent genus. Following the popular book by Gómez-Bustillo & Fernández-Rubio (1974) the Iberian species of the genus are *Agrodiaetus damon, A. dolus, A. fabressei* (Oberthür, 1910), *A. ripartii* and *A. ainsae* Forster, 1961, to which *A. violetae* Gomez-Bustillo, Expósito & Martínez, 1979 was added later as a new species. *A. fabressei* corresponds to what Agenjo (1947) named *P. admetus,* now known to be restricted to Eastern Europe and Asia Minor. There is a tendency to split the species of the group into new species whose validity has been discussed in several reviews (see for example Fernández-Rubio, 1992). Higgins (1975) also considers within the genus the species *A. amanda* (Schneider, 1792), *A. thersites* (Cantener, 1834) and *A. escheri* (Hübner, [1823]), but although this inclusion has strong arguments in its favour, the resulting genus is less homogeneous. Kudrna (1986 : 161, 229-231) in the latest European checklist grouped the *Agrodiaetus* within the genus *Polyommatus* and listed the following species as present in Spain : *P. ainsae, P. damon, P. dolus, P. fabressei, P. ripartii,* and *P. violetae.* The first three taxa have blue males and the last three brown males. The inclusion of *Agrodiaetus* in *Polyommatus* is not supported by recent research (Lelievre, 1992) and we do not assume it for simplicity.

We centered our study only in the *Agrodiaetus* sensu stricto group (following Higgins & Riley, 1970), but excluded *A. damon* which is a fairly distinct species that has never been mistaken with the others anywhere in its range. The objectives of our study were to identify the specific entities of the *Agrodiaetus* group living in the Iberian Peninsula based on cytotaxonomical and morphological information and to give accurate UTM distributions for every species.

Materials and methods

Chromosome number studies were made on male testes of at least five specimens for each species and/or geographical area. Testes were dissected *in situ* under a stereomicroscope in distilled water and fixed with a solution of ethanol : acetic acid (3:1). They were kept at ca. 5°C until analysis was possible. After staining the samples with lacto-propionic orceine they were observed under a phase contrast microscope to count chromosomes using the squash technique (Lorkovic, 1990) with small fragments of the testes. Brown males were studied from Sierra de Cazorla (SW Spain), Sistema Ibérico (Central Spain), Catalonia (NE Spain) and the Cantabrian Mountains (N Spain). Blue males were studied from Catalonia and the Pyrenees. This covered all the taxa previously described and the geographic range of the group in the Iberian Peninsula and was considered enough to give an idea of the chromosome numbers for each area and species.

Distribution data were collected using faunistic records from the literature and from specimens in the collections of the following Spanish institutions : Museo Nacional de Ciencias Naturales, Sociedad de Ciencias Naturales Aranzadi, Museo de Ciencias Naturales de Vitoria, Museo de Zoología de Barcelona and Universidad Autónoma de Madrid. Private collections from Fidel Fernández-Rubio, José Luis Yela, Arcadi Cervelló, José María Font and José Luis Nuñez and personal communications from Albert Masó, José Bellavista and Francisco Abós were used for distribution records. Data were also gathered visiting a total of 36 localities from 12 different Provinces in which specimens were taken for morphological analysis. The specimens used for this study are preserved in the zoological collection of the Universidad Autónoma de Madrid (UAMZ). A database was created to process all the faunistic data with information on localities, provinces, dates, UTM coordinates, altitudes and bibliographic references. This is available upon request for anyone interested, but its volume (more than 700 records) made its inclusion in this paper impossible.

Maps were produced using a commercial program for automated cartography (CYANUS) for the Iberian Peninsula and Balearic Islands. Each record was assigned to a particular species using karyological data for the localities from which chromosome studies were made. For the rest of the localities identification was based on geographical and morphological affinities with the former records. The morphological analysis of the records for which we had specimens, showed that the individuals identified by this method had the typical morphology of the species to which they were assigned.

The biology of the group was studied at the different localities visited, where we gathered data on foodplants, overwintering stages and immature stage morphology.

Table 1

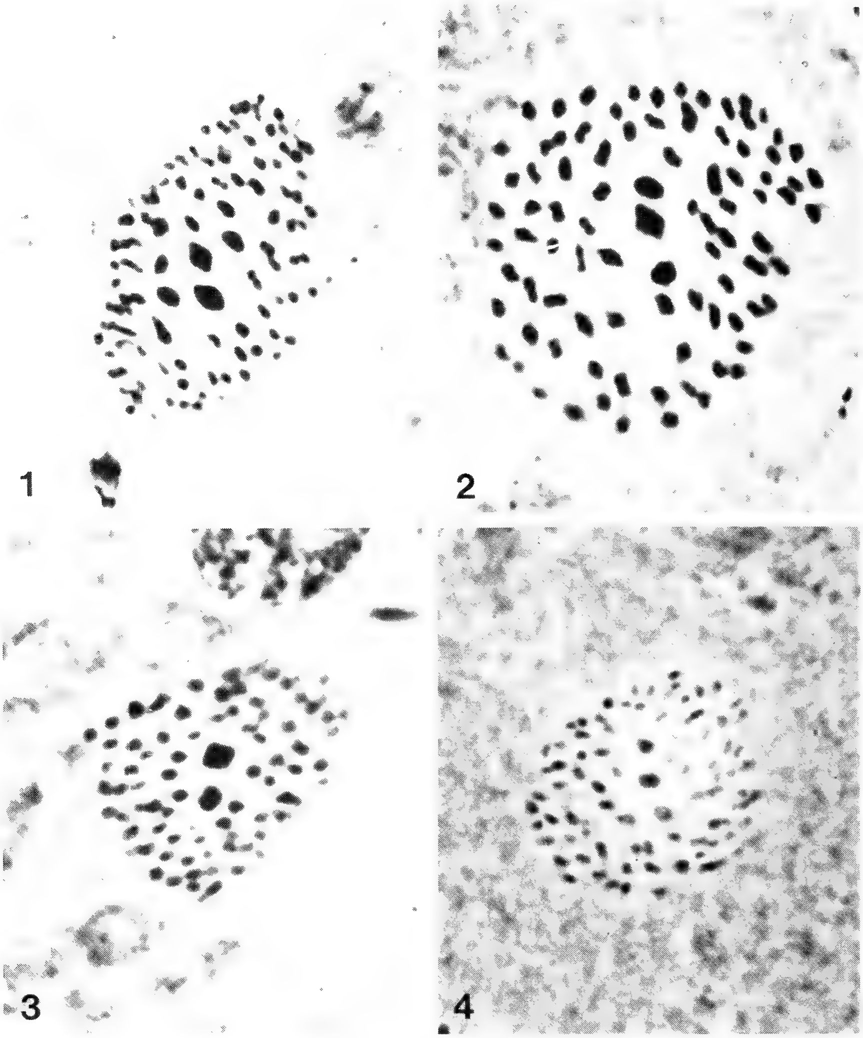
Localities, sample size and chromosome numbers of the studied material and all the literature references for *Agrodiaetus* species in the Iberian Peninsula. "No. males" refers to the number of males that produced metaphase I plates suitable for chromosome counts and the total sample is given in brackets. References are as follows : (1) de Lesse, 1960b (2) de Lesse, 1961a (3) de Lesse, 1962 (4) de Lesse, 1968 and (*) our own observations

Locality	**Province**	**No. males**	**Chr. No.**	**Macrochr.**	**Species**	**Ref.**
Villanueva	Burgos	2	108	?	*ainsae*	3
Peñahorada	Burgos	1 (1)	?	2	*ainsae*	*
Bernués	Huesca	3	108-110	?	*ainsae*	3
Jaca	Huesca	1 (2)	—	—	*ainsae*	*
Taradell	Barcelona	3 (5)	103	6	*fulgens*	*
Noguera	Teruel	8	90	4	*fabressei*	1
Albarracín	Teruel	1 (9)	—	—	*fabressei*	*
Peñalén	Guadalajara	1 (2)	90	3	*fabressei*	*
Cazorla	Jaén	6 (12)	90	3	*fabressei*	*
Morella	Castellón	1	90	4	*fabressei*	2
Villarroya	Teruel	1	90	4	*fabressei*	2
Olocan	Castellón	2 (15)	90	2	*ripartii*	2
Amorós	Barcelona	4	90	2	*ripartii*	4
Collsuspina	Barcelona	1 (2)	ca. 88	2	*ripartii*	*
Taradell	Barcelona	3(10)	ca. 88	2	*ripartii*	*
Santa Coloma	Tarragona	0 (2)	—	—	*ripartii*	*
Peñahorada	Burgos	1 (6)	90	2	*ripartii*	*
Gredilla	Burgos	2 (5)	ca. 85-90	2	*ripartii*	*
Jaca	Huesca	1 (2)	ca. 88	2	*ripartii*	*
Jaca	Huesca	?	?	2	*ripartii*	2

Results

Chromosome numbers in different populations

Table 1 gives a summary of the data from our study pooled with data from de Lesse's 1960b, 1961a, 1962 and 1968 papers. From these results it is clear that the best genetic marker for the identification of the species of the group in the Iberian Peninsula is the number of macrochromosomes (see White, 1973 for the use of the term, that appears as "gros chromosomes" in de Lesse, 1960b). These can be defined in Lepidoptera as chromosomes with two to four times the normal size, located in the centre of metaphase I plates and surrounded by normal-sized chromosomes (Figs 1-4). The location of macrochromosomes contrasts with their peripheral location in Orthoptera, amphibians and reptiles (White, 1973). In lycaenids the number of macrochromosomes is always low while in the other groups it usually outnumbers that of microchromosomes (see White, 1973 for compa-



Figs 1-4. Metaphase I plates. 1 — *Agrodiaetus fulgens.* (Taradell, Barcelona Province, type locality for species) n = 103, six macrochromosomes ; 2 — *Agrodiaetus fabressei* (Peñalén, Guadalajara Province), n = 90, three macrochromosomes ; 3 — *Agrodiaetus ripartii* (Collsuspina, Barcelona Province), n = ca. 88, two macrochromosomes ; 4 — *Agrodiaetus fabressei violetae* (Sierra de Cazorla, Jaén Province), n = 90, three macrochromosomes.

rison), and it is probable that these configurations depend on mechanical aspects of the cell division process. The number of chromosomes is also distinctive, but the metaphase I plates of *Agrodiaetus* have large chromosome numbers and accurate counts are difficult in most cases. The results from Table 1 support the following species' arrangements : *A. ainsae* with n = ca. 108 lives in the Pyrenees and a wide area surrounding the Cantabrian Mountains, whereas in Catalonia the specimens previously assigned to *A. dolus* should now be considered a distinct species. The name *A. fulgens* (Sagarra, 1925) is valid for this species, because it was given to what was thought a subspecies of *A. dolus* in the same localities where the samples for chromosome studies were taken. The reason for considering *fulgens* a distinct species is the different chromosome number (n = ca. 103, while *dolus* has n = 124 and *ainsae* n = 108) and above all, the different number of macrochromosomes of these specimens (six for *fulgens* (Fig. 1) as opposed to four in *dolus*, DE LESSE, 1961b). de Lesse (1962, 1966) only gives the chromosome number for *A. ainsae* and does not provide figures for it, but our specimen from Peñahorada (Burgos Province, northern Spain) had two macrochromosomes although the metaphase I plates we obtained were not suitable for accurate chromosome counts. The number of macrochromosomes is therefore six in *A. fulgens*, four in *A. dolus* and two in *A. ainsae*. Although our sample for *fulgens* is very small (only 3 specimens with metaphase I plates), the separation of *ainsae* from *dolus* was made with similar samples (five specimens, DE LESSE, 1962). Moreover it is not chromosome number, but the number of macrochromosomes that we consider to be a strong argument to split *fulgens* from *ainsae*, because it is highly improbable that specimens with such a different chromosome morphology can belong to the same species.

A. ripartii and *A. fabressei* share the same chromosome number (n = 90) but clearly differ in the morphology of chromosomes, *fabressei* having three (Fig. 2) and *ripartii* two (Fig. 3) macrochromosomes. DE LESSE (1960a, Table 1) states that *fabressei* has four macrochromosomes, but after examining our photographs and drawings we have concluded that the species clearly has three large chromosomes constantly seen in all the metaphase I plates. The difference between de Lesse's results and ours is due to the existence of one or two medium sized chromosomes that in some plates resemble macrochromosomes, but are driven out of the centre of the spindle in a majority of our figures from *fabressei*. Large chromosomes are always located in the centre of metaphase I plates, and they are easily spotted when comparing long series of plates. This has been possible with the material from the Sierra de Cazorla, previously regarded as *A. violetae*, where the presence of three macrochromosomes is clear (Fig. 4). The latter race has therefore a true *fabressei* karyotype, which supports the idea outlined in Fernández-Rubio (1992) that it is a subspecies of *fabressei* and not of *ripartii*, as has been proposed (Balletto, pers. comm.). The distribution of both karyotypes seems to be clearcut from the data in Table 1. *A. ripartii* is a species living from the Cantabrian Mountains to the Catalonian Pyrenees whereas *A. fabressei* lives in central Spain and in some southern mountain ranges.

Morphology

There is not a single character clearly separating all *ripartii* specimens from *fabressei*, and *ainsae* from the Catalonian species *fulgens*. In the first case a group of characters can identify most of the specimens, but in the latter this proves to be very difficult. Generally speaking *fabressei* lacks the white band along the v4 on the hind wing's underside, but there is a great variability on this character. Traditionally brown males without the white band have been regarded as *fabressei*, and this has produced records of the species in the Pyrenees (Gómez, 1988) and Catalonia (Gómez-Bustillo & Fernández-Rubio, 1974). The book by Manley & Allcard (1970) is unusual because it illustrates an individual with white band taken at Peñahorada (Burgos Province) under the name *fabressei* and a very similar specimen (with white band) from Albarracín (Teruel) as *ripartii*. These identifications are in disagreement with our karyological results. On the other hand a white band is also present in some *fabressei* specimens leading some authors to consider these as *ripartii* (Gómez-Bustillo & Fernández-Rubio, 1974 ; Manley & Allcard, 1970 for the male collected in Albarracín, Teruel). The Catalonian race *agenjoi* Forster, 1965 has been considered a different species (Higgins & Hargreaves, 1983), a subspecies of *fabressei* (Manley & Allcard, 1970 ; Gómez-Bustillo & Fernández-Rubio, 1974) or a subspecies of *ripartii* (Agenjo, 1964 ; de Lesse, 1968, Pérez, 1979). Black spots on the underside are larger in *fabressei* than in the normal *ripartii*, but again the Catalonian specimens are an exception to this and resemble typical *fabressei*. Another distinctive feature of *fabressei* has traditionally been the enlargement of the black spot between v2 and v3 in the forewing's underside (de Lesse, 1968), but our material from the whole geographic range of both species does not support the distinctness of this feature. The apical angle of the forewing is smaller in *fabressei* than in *ripartii*. Althoug this seems to be a constant character, it is hard to measure and by itself is not useful enough to identify all the specimens clearly. The third supposed species with brown males, *A. violetae*, has a mixture of morphological characters from *ripartii* and *fabressei* with a white band in the underside of the hindwing (absent in six of our sample of 22 butterflies) and a small angle in the apex of the forewing. As a result of its chromosome morphology we consider it a subspecies of *A. fabressei.* Although there are exceptions to all the characters mentioned above, most of the specimens can be identified by a mixture of characters. Therefore specimens without white band in the underside, large spots in the underside and small apical angle can be considered *fabressei*, provided they are in the distribution range of the species. Individuals outside the normal species' range need chromosome study to be sure of their identity.

As far as the species with blue males is concerned identification is also difficult. *A. fulgens* has traditionally been regarded as a race with brighter blue and lack of the white band in the hindwing's underside. These two features are useful for most specimens, but again a substantial morphological variation takes place in *ainsae* for both characters, making individual diagnosis difficult in some cases.

Distribution

Given that it is very difficult to identify the species of the group based on morphological features, we considered the possibility to use both chromosome numbers and distribution data to assign a given individual to a species of the group. In almost all the studied northern localities, three *Agrodiaetus* species live together : *damon*, which is a well characterized distinct species, a species with blue males and a species with brown males. We assumed that each area has a single brown and/or blue species (this was confirmed by the chromosome study) and by mapping the species tried to define areas isolated by barriers separating species. In the localities of the Sistema Ibérico (Central Spain) only a species with brown males flies together with *damon* and the chromosome studies revealed this to be *fabressei* (de Lesse, 1960b, and our observations, Table 1).

A. fabressei (Fig. 5) is therefore restricted to the Sistema Iberico, a mountain range running from north to south in Central Spain and to the Sierras of Andalusia. The species lives in the Serranías of Cuenca and Albarracín, the high plains of La Alcarria, some calcareous outcrops in Segovia Province and north of Madrid, and reaches the Province of Soria in the north, being isolated from *ripartii* by the Picos de Urbión, whose northern slopes flow down to the Ebro Valley. *A. fabressei violetae* is found in a total of twelve UTM squares (10 × 10 km)

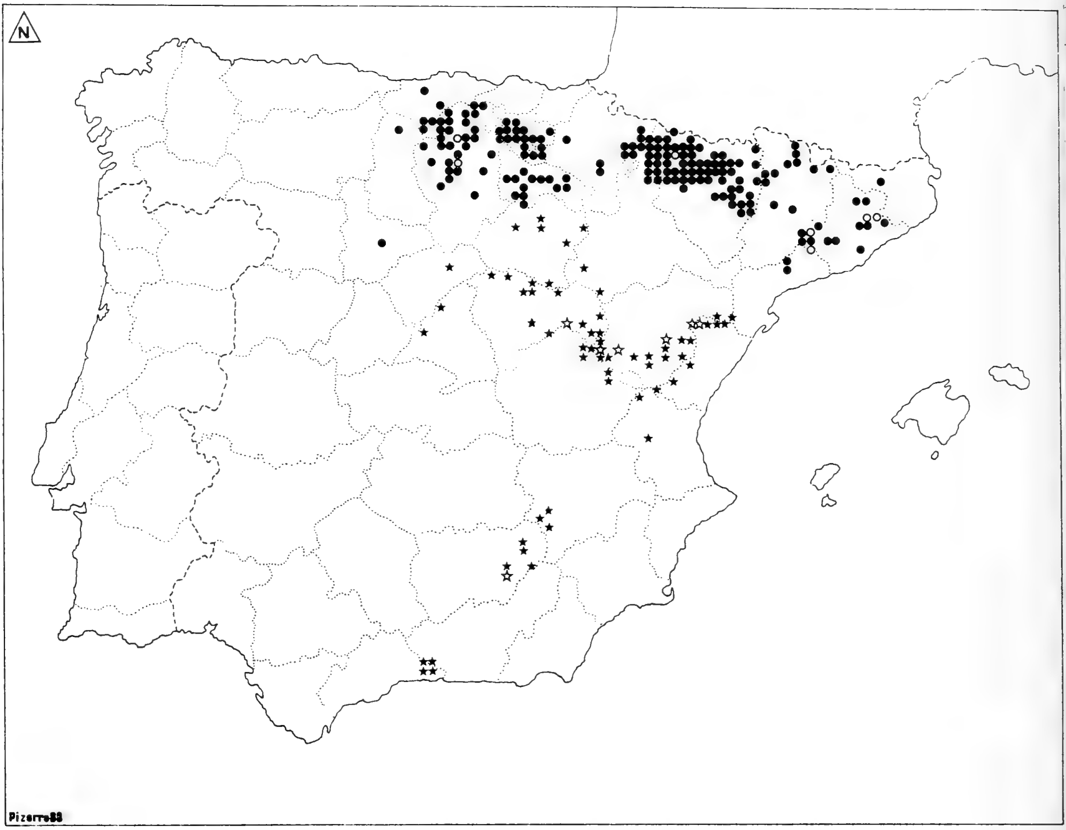


Fig. 5. Distribution of *Agrodiaetus ripartii* (circle) and *A. fabressei* (star) in the Iberian Peninsula. Each symbol represents the presence of the species in a 10 × 10 km UTM square. Open symbols represent localities where chromosome studies were available.

from four mountain ranges in Southern Spain (Sierra Tejeda, Sierra de Almijara, Sierra de Cazorla and Sierra de Alcaraz).

A. ripartii (Fig. 5) lives over a wide area, from Catalonia through the Pyrenees to the Cantabrian Mountains, where it lives mainly on the southern slopes. Two subspecies can be distinguised: the Catalonian *agenjoi* and the Pyrenean and Cantabrian *ripartii*, separated by an area that more or less matches the boundary between the Pyrenees and a mountain range running from north to south in eastern Catalonia (Serralada Vertical) in which the species becomes scarce (Fig. 5). DE LESSE (1961a) describes the presence of specimens with a typical *ripartii*

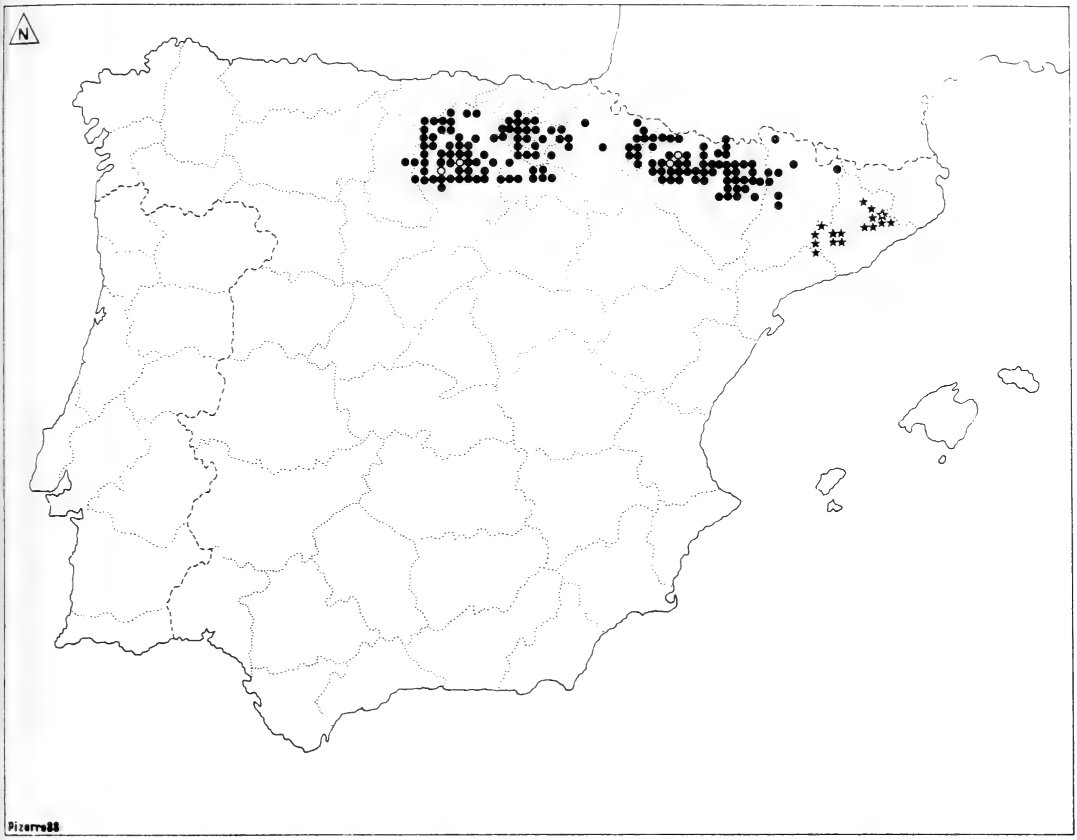


Fig. 6. Distribution of *Agrodiaetus ainsae* (circle) and *A. fulgens* (star) in the Iberian Peninsula. Each symbol represents the presence of the species in a 10 × 10 km UTM square. Open symbols represent localities where chromosome studies were available.

karyotype in Olocau del Rey (Castellón Province), an area where *fabressei* is widespread. If this finding is confirmed it may be possible that *ripartii* has some populations more or less mixed with *fabressei* colonies in this contact zone.

A. ainsae (Fig. 6) is the most widespread species with blue males in this area. Specimens from the western Pyrenees and the Cantabrian mountains belong to this species, but not a single locality has been found south to the Picos de Urbión, suggesting that the southern limit for *ripartii* is also valid for the blue species of the group.

A. fulgens (Fig. 6) has until now been considered a subspecies of *dolus* (Gómez-Bustillo & Fernández-Rubio, 1974, Higgins, 1975). It has only been cited from a handful of localities in Catalonia and between the strongholds of this species and the previous one there is a wide area with scarcity of records that can be seen when the distribution of both species is plotted together (Fig. 6). It should be noted that this lack of records is not a consequence of lack of information, for this is a well explored area.

Biology

All the studied species use *Onobrychis* as larval foodplants. In the Catalonian localities, the Pyrenees, the Sistema Ibérico and the Cantabrian Mountains the foodplant is always *O. viciifolia* Scop. The only population that uses a different foodplant is *A. fabressei violetae* in the Sierra de Cazorla. Its foodplant is *O. argentea* Boiss., but we do not consider this difference to be relevant with respect to its taxonomic status, because the two plants are ecologically similar, and *O. argentea* is the only species of this plant genus living in Sierra de Cazorla. In all other aspects the biology of the studied species is very similar. They all overwinter as third instar larvae (we studied this for *fabressei, ripartii* and *ainsae*) and pupate during the spring at the base of the foodplant. The fullgrown larva is very similar in species living in the same area. Thus we were unable to distinguish between *A. fabressei* and and the very different *A. damon* in Albarracín (Teruel Province), and between *A. ripartii* and *A. ainsae* in Jaca (Huesca Province). All the larvae have tentacles and dorsal nectary organs (Newcomer's gland), and the coloured band in the lateral zone of the larva can have different colours, being yellow in the specimens from Jaca in the Pyrenees and pink in the larvae from Albarracín. Wether this can be a distinctive feature between *ripartii* and *fabressei* or just a character related to the ecological peculiarities of the site requires a more comprehensive study. Egg morphology is being studied under the SEM microscope by two of us (Munguira & Martín, in preparation) and all the species exhibit a very similar chorionic pattern, with no distinctive features among them.

Discussion

Previous results have shown how complicated a taxonomic study of this difficult butterfly group can be. Although butterfly taxonomy in Europe is often regarded as being settled, there are some groups in which a great deal of research is still needed. Two of the main taxonomic groups within which the boundaries between species are not yet well defined are found in *Agrodiaetus*, and *Polyommatus (Lysandra)* of the *coridon* (Poda, 1761) group (DE BAST, 1985 ; MENSI *et al.*, 1988 ; LELIEVRE, 1992).

Our approach to the taxonomy of the group was to begin to identify the different karyotypes found in the Iberian Peninsula. Then we tried to study as many areas as possible to assign karyotypes to relevant areas from the biogeographical point of view. Plotting this information with distribution maps, we tried to draw accurate maps of every species. The separation of species in contact areas such as the boundaries between *A. ainsae* and *A. fulgens* is still tentative and a karyological study of almost every locality is needed to be completely sure. The limit between *A. ripartii* and *A. fabressei* also needs some further study, but in this case we think that our proposal is closer to reality because the morphology of specimens from Abejar (Soria) resembles the typical *fabressei*, with most butterflies lacking the white band on the hindwing's underside (MANLEY & ALLCARD, 1970). On the other hand the specimens from the northern slopes of the Sistema Ibérico (e. g. Castañares de las Cuevas in La Rioja) are morphologically true *ripartii* with the white band present in all the studied material. Some research needs to be done on the identity of some populations close to the town of Morella in central eastern Spain, where DE LESSE (1961a) identified karyotypes belonging to *fabressei* and *ripartii* in nearby populations, but never in the same one. This area may prove to be a contact zone for the two species, and the segregation of populations may not be as clearcut as depicted in the distribution maps. In a locality between the towns of Olocan and Forcall, de Lesse (1961a) found males with a typical *ripartii* karyotype and a single male with *fabressei* morphology, for which a chromosome study was not possible. Speaking of this *fabressei* specimen he writes that "on a vu qu'aucun doute ne peut exister sur son identité". Therefore a contact area between the two species might exist in Morella, but this statement has to be proven through more chromosomic studies. On the other hand, although some authors have reported the two species from the same locality, nobody has yet identified specimens of the two different karyotypes living together.

Populations having different chromosome numbers are usually thought to belong to different species. Although DE LESSE (1960a ; 1966) is very cautious to split species by their distinct chromosome numbers, his data have always been used as a proof to make new species' arrangements (GÓMEZ-BUSTILLO & FERNÁNDEZ-RUBIO, 1974 ; HIGGINS, 1975). Some intraspecific variation in chromosome numbers and chromosome morphology can not be plainly rejected (White, 1973), particularly in such similarly looking and difficult groups as the *Agrodiaetus*. Nevertheless, before a more thorough study is done on the significance of chromosome number variability in the evolution of lycaenids, we assume it is safer to assign populations with different chromosome numbers to different species. This approach was made in most chromosomic studies in butterflies, as for example to support the separation of *A. humedasae* (Troiano, *et al.*, 1979), to split a species complex in several species previously regarded as identical (Soumalanien & Brown, 1984) or as a general rule to explain chromosome number variability (see White, 1973). On the other hand a karyological feature of great taxonomic importance has emerged during our study : the variability of the number of macrochromosomes observed in the centre of metaphase I plates. This character was previously used by de Lesse (1960b), but our data prove that it is the best genetic marker to identify the species of *Agrodiaetus* in the Iberian Peninsula. We can therefore recognize *fulgens* by its six macrochromosomes and separate it from *ainsae* that has only two, whereas the species with brown males differ in having two (*ripartii*) or three (*fabressei*) of these large chromosomes.

As a conclusion to our study, the Spanish *Agrodiaetus* with their chromosome numbers and distribution are : *A. ripartii* ($n = 90$, two macrochromosomes) living from Catalonia to the Cantabrian Mountains, *A. fabressei* ($n = 90$, three macrochromosomes) living in the Sistema Ibérico (South to the Picos de Urbión), the limestone outcrops of Central Spain and some southern mountain ranges (Sierra Almijara, Cazorla, Alcaraz and Tejeda), *A. ainsae* ($n = 108$, two macrochromosomes) from the Pyrenees and Northern Spain and *A. fulgens* ($n =$ ca. 103, six macrochromosomes) living in Catalonia.

Acknowledgements

We are very grateful to Fidel Fernández-Rubio, Arcadi Cervelló, José María Font, José Luis Nuñez and José Luis Yela for kindly giving access to their private collections. Isabel Izquierdo, Ibón de Olano and Jesús Aldaba gave facilities for the revision of public collections and Albert Masó and Francisco Abós provided unpublished distribution records. José Serrano and Jaime Gosalvez helped us in many ways with cytogenetical analysis, discussion of data and giving access to their laboratories. Enrique García-Barros made valuable suggestions to a previous draft of the manuscript.

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Illustrierter Bestimmungsschlüssel für die Präimaginalstadien der Schwärmer Europas und Nordafrikas (Lepidoptera, Sphingidae)

Teil II : Eilarven

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Summary

Keys to the preimaginal instars of the hawkmoths of Europe and North Africa (Lepidoptera, Sphingidae). Part II : First instar larvae.
This is the second of a small series of keys dealing with mature larvae, first instar larvae, and pupae. They aim at the identification of living specimens. Therefore, all characters that are not visible in the intact animal are omitted. It is hoped that the keys will be useful for faunistic purposes and for research in the ecology of hawkmoths.

Zusammenfassung

Dieser Schlüssel ist der zweite aus einer kleinen Reihe, die sich mit den erwachsenen Raupen, den Eilarven und den Puppen befaßt. Sein Ziel ist das Bestimmen lebender Tiere. Daher wird auf alle Merkmale, die am lebenden Tier nicht erkennbar sind (z.B. Mandibelformen), bewußt verzichtet. Die Schlüssel könnten vor allem in der Faunistik und für die ökologische Forschung von Nutzen sein.

Résumé

Cette clé est la deuxième d'une petite série qui traite des chenilles — adultes et au stade L1 — et des chrysalides. Elle a pour objectif de permettre la détermination des espèces vivantes à ces différents stades. Par conséquent ne sont pas pris en considération les caractères invisibles chez l'animal vivant (p. ex. la forme des mandibules). Ces clés pourraient rendre service en faunistique et pour les recherches sur l'écologie des Sphingidae.

Einleitung

Eilarven verschiedener Schmetterlingsgruppen sind bisher vorwiegend zur Klärung der Systematik herangezogen worden (z.B. Wasserthal, 1970). Die hier wichtigen Merkmale sind jedoch in der Regel erst nach dem Töten des Tieres erkennbar und daher für eine einfache Artbestimmung vielfach ungeeignet.

Eilarven sind bereits in der Frühzeit der wissenschaftlichen Entomologie ein beliebtes Studien- und Mikroskopierobjekt gewesen (Weismann, 1876 ; Poulton, 1885 ; 1886 ; 1888 ; Gillmer, 1904 ; Denso, 1906a,b). Auch in den letzten Jahren sind Eilarven etlicher Schwärmer beschrieben worden (z.B. Heinig, 1976 ; 1978 ; 1981 ; Harbich, 1978 ; Pittaway, 1979 ; Pelzer, 1982 ; Heinig & Häsler, 1986 ; Freina, 1994). Auf die Merkmale, durch die sich verwandte Arten unterscheiden, gehen die Beschreibungen jedoch nur in Ausnahmefällen ein (Pelzer, 1988).

Von einfachen Bestimmungsschlüsseln für die Präimaginalstadien, mit denen sich bereits ein lebendes Tier bestimmen läßt, könnte neben der Systematik besonders die Faunistik profitieren ; im faunistischen Schrifttum tauchen Eilarven als Artnachweis bisher nicht auf. Dabei sind Eier oder Eilarven manchmal nicht schwieriger zu finden als die Falter (z.B. Pelzer, 1982). Könnte man bereits die Eilarve bestimmen, bräuchte man das fragliche Tier nicht bis zur erwachsenen Raupe oder gar bis zum Falter aufzuziehen — was auf Exkursionen in der Regel nur selten möglich sein dürfte.

Die Bestimmung von Eilarven ist in vielen Fällen erstaunlich einfach. Im Gegensatz zu erwachsenen Raupen weisen sie nämlich nur eine sehr geringe Variabilität auf. Andererseits wirkt die insgesamt nur kleine Zahl verwertbarer Merkmale jedoch limitierend.

Systematik, geographische Abgrenzung, Material und Methoden

Die verwendete Systematik wird im 1. Teil der Reihe erläutert (Pelzer, 1991) ; sie folgt weitgehend der Auffassung von Rothschild & Jordan (1903). Der Name *Laothoe tremulae* (Fischer von Waldheim, 1830) wird durch *L. amurensis* (Staudinger, 1892) ersetzt (Pittaway, 1993).

⟶

Abb. 1-6. Eilarven europäischer und nordafrikanischer Schwärmer. In Klammern hinter dem Artnamen der jeweilige Abbildungsmaßstab.

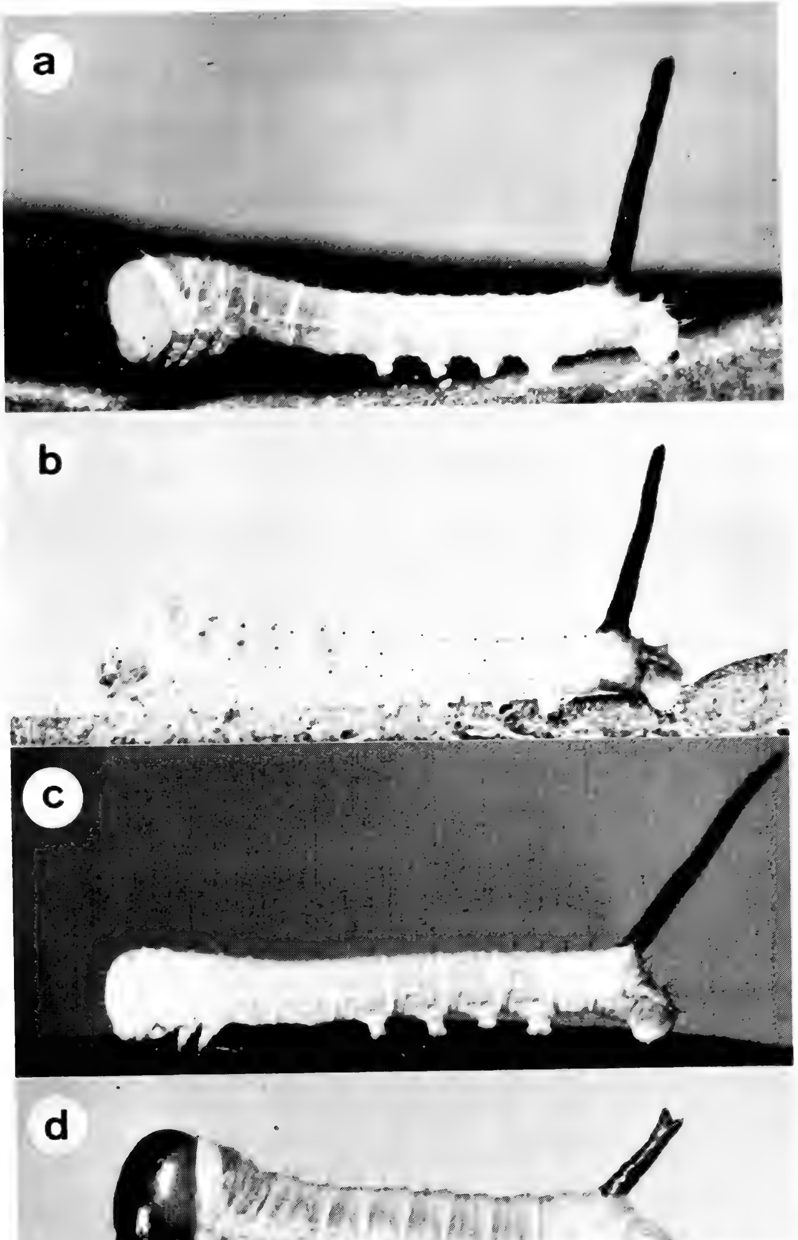

Abb. 1. a) *A. atropos* (14 ×) ; b) *A. convolvuli* (21 ×) ; c) *S. ligustri* (12 ×) ; d) *H. pinastri* (19 ×).

Tab. 1.
Schwärmerarten Europas und Nordafrikas

Acherontia atropos (Linné, 1758)	Totenkopf
Agrius convolvuli (Linné, 1758)	Windenschwärmer
Sphinx ligustri Linné, 1758	Ligusterschwärmer
Hyloicus pinastri (Linné, 1758)	Kiefernschwärmer
Dolbina elegans A. Bang-Haas, 1912	
Marumba quercus (Denis & Schiffermüller, 1776)	Eichenschwärmer
Mimas tiliae (Linné, 1758)	Lindenschwärmer
Smerinthus caecus Ménétriés, 1857	
Smerinthus ocellatus (Linné, 1758)	Abendpfauenauge
Laothoe populi (Linné, 1758)	Pappelschwärmer
Laothoe amurensis (Staudinger, 1892)	
Hemaris fuciformis (Linné, 1758)	Hummelschwärmer
Hemaris tityus (Linné, 1758)	Skabiosenschwärmer
Hemaris croatica (Esper, 1779)	
Daphnis nerii (Linné, 1758)	Oleanderschwärmer
Macroglossum stellatarum (Linné, 1758)	Taubenschwanz
Proserpinus proserpina (Pallas, 1772)	Nachtkerzenschwärmer
Rethera komarovi (Christoph, 1885)	
Sphingonaepiopsis gorgoniades (Hübner, 1819)	
Hyles lineata (Fabricius, 1775)	Linienschwärmer
Hyles gallii (Rottemburg, 1775)	Labkrautschwärmer
Hyles euphorbiae (Linné, 1758)	Wolfsmilchschwärmer
Hyles nicaea (Prunner, 1798)	Nizzaschwärmer
Hyles centralasiae (Staudinger, 1887)	
Hyles zygophylli (Ochsenheimer, 1808)	
Hyles hippophaes (Esper, 1789)	Sanddornschwärmer
Hyles vespertilio (Esper, 1779)	Fledermausschwärmer
Deilephila elpenor (Linné, 1758)	Mittlerer Weinschwärmer
Deilephila porcellus (Linné, 1758)	Kleiner Weinschwärmer
Hippotion celerio (Linné, 1758)	Großer Weinschwärmer
Hippotion osiris (Dalman, 1823)	
Theretra alecto (Linné, 1758)	

Das im Schlüssel behandelte Gebiet umfaßt Europa bis zum Ural sowie Nordafrika nördlich der Sahara. Nach dem gegenwärtigen Kenntnisstand treten 32 Schwärmerarten mehr oder weniger regelmäßig in diesem Areal auf (Tab. 1). Hinzu kommen einige Irrgäste aus Nordamerika, Afrika und Asien, die hier nicht behandelt werden (Listen in Meerman, 1987 und Pittaway, 1993). Die Merkmale der wenigen Hybriden, die aus dem Freiland bekannt sind, vermitteln stets zwischen denen der Elternarten.

Die Schlüssel basieren ausschließlich auf eigenen Daten. Sie beruhen auf zahlreichen Zuchten und Freilandbeobachtungen der meisten hier behandelten Arten. Von fünf Arten lag mir allerdings kein Material vor. Es handelt sich dabei um Arten, für die Europa auf dem äußersten Rand ihres Verbreitungsgebiets liegt.

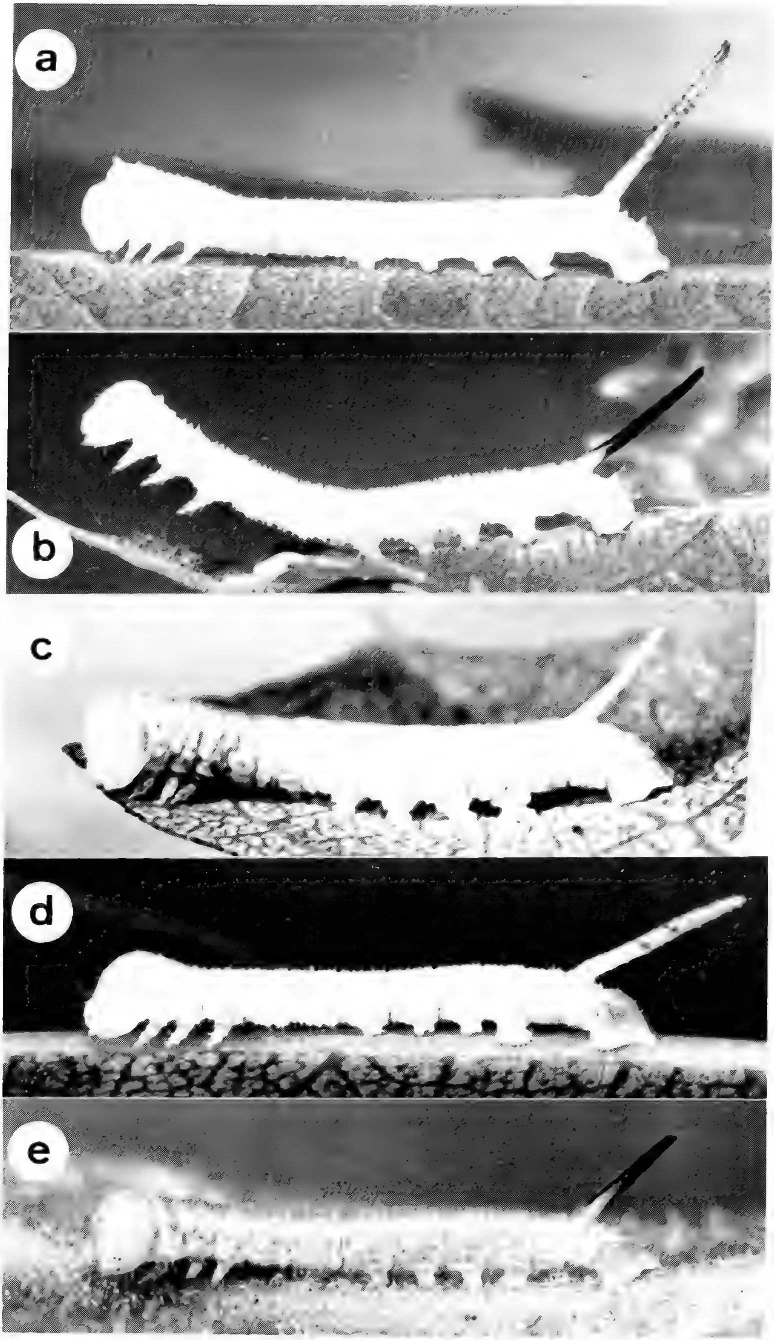

Abb. 2. a) *M. quercus* (8 ×) ; b) *M. tiliae* (12 ×) ; c) *L. amurensis* (11 ×) ; d) *L. populi* (11 ×) ; e) *S. ocellatus* (14 ×).

Die Aufnahme von *R. komarovi* in den Schlüssel erfolgt nach einem Farbdia, das mir Prof. Dr. L.T. Wasserthal (Erlangen) dankenswerterweise überlassen hat. Die noch unbeschriebene Eilarve von *S. caecus* dürfte der von *S. ocellatus* sehr ähneln. Aus der einzigen, mir vorliegenden Beschreibung der Eiraupe von *D. elegans* geht lediglich hervor, daß sie ein Horn besitzt (SOFFNER, 1959). Hier und bei den Arten *S. gorgoniades* und *H. osiris* kann — anders als bei den erwachsenen Raupen — nicht abgeschätzt werden, wo im Bestimmungsschlüssel man vermutlich ankäme.

Zur Bestimmung ist eine Handlupe mit wenigstens 10-, besser 20facher Vergrößerung notwendig. Zur Ermittlung des Horn-/Afterklappenlängen-Verhältnisses (H/A, s.u.) besonders geeignet sind Meßlupen mit eingearbeiteter Millimeterskala, wie sie von Briefmarkensammlern verwendet werden.

Einfache Längenangaben, wie z.B. die Gesamt-Körperlänge, sind als Bestimmungsmerkmal gewöhnlich ebenso unbrauchbar wie simple Farbangaben. Bei einigen Arten werden einige Zeit nach Beginn der Nahrungsaufnahme Zeichnungselemente des zweiten Stadiums mehr oder weniger deutlich sichtbar. Solche variablen Merkmale werden nicht berücksichtigt.

Die Färbung der Hartteile ändert sich dagegen während eines Stadiums nicht und ist daher für die Bestimmung geeignet. Auch die Beweglichkeit des Horns ist ein gutes Merkmal: manche Arten können ihr Horn weit nach vorn neigen (Abb. 3d), bei anderen ist es praktisch unbeweglich. Wo die Futterpflanzen der Raupen bei der Bestimmung helfen können, werden sie mit aufgeführt.

Ein „mathematisches“ Merkmal hat sich als besonders einfach und brauchbar erwiesen: das Verhältnis der Hornlänge relativ zur Länge der Afterklappe (Horn-/ Afterklappen-Längenverhältnis, H/A). Dieses Längenverhältnis läßt sich schon rein optisch gut abschätzen. Bei der Kiefernschwärmerraupe auf Abb. 1d beträgt es etwa 1, d.h. Horn und Afterklappe sind etwa gleich lang. Das Schwanzhorn ist bei Eilarven — sofern es nicht beim Schlupf verbogen worden ist — immer gerade. Zur Ermittlung von H/A ist stets die Gesamtlänge des gestreckten Horns zu verwenden.

Die Anordnung der einzelnen Arten auf den Tafeln weicht z.T. von der in Teil I ab, um ähnliche Raupen direkt nebeneinander zu stellen.

Da die lebenden Eilarven einiger Arten bei Lupenvergrößerung nur schwer zu bestimmen sind, gibt ein **Hilfsschlüssel** zusätzlich Unterscheidungsmerkmale des zweiten Raupenstadiums an.

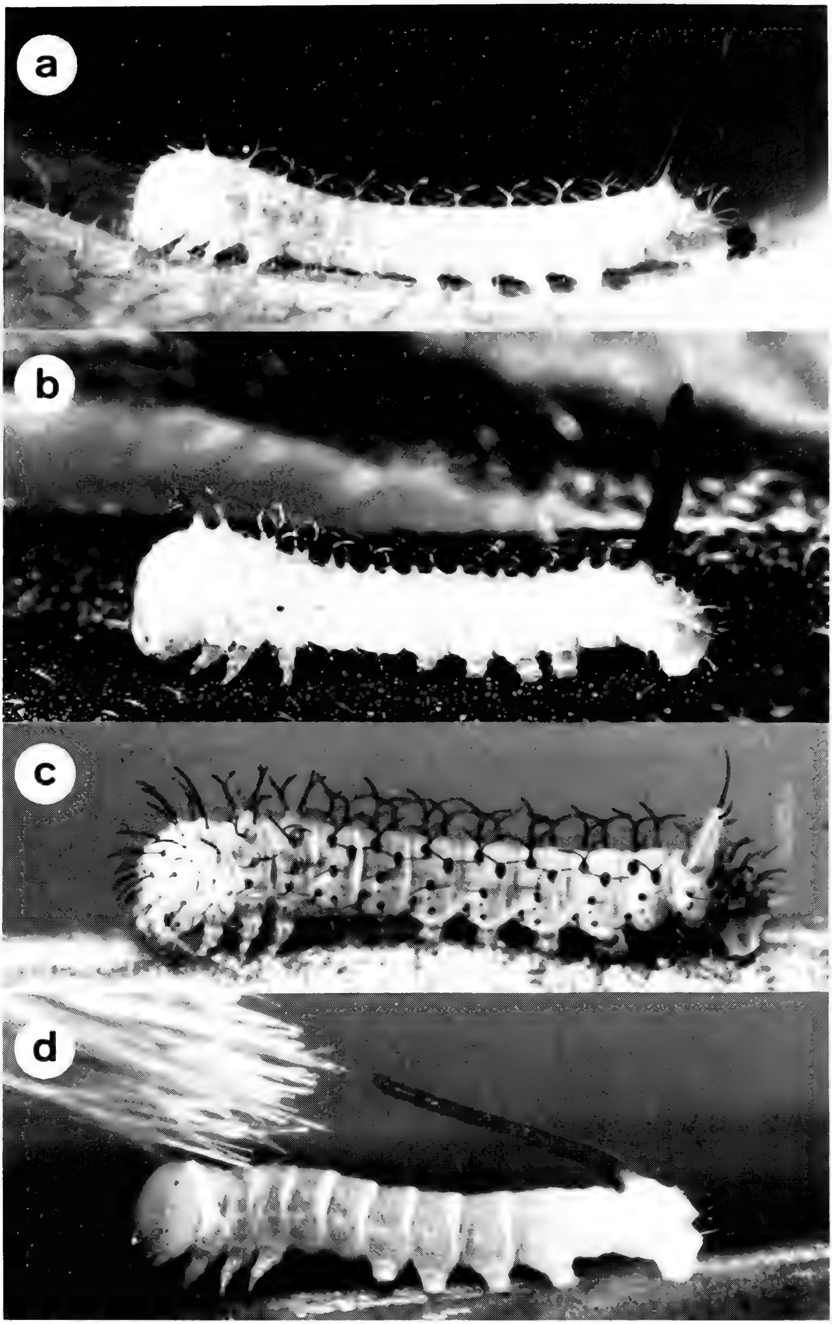

Abb. 3. a) *H. fuciformis* (20 ×) ; b) *H. croatica* (22 ×) ; c) *H. tityus* (22 ×) ; d) *D. nerii* (16 ×).

Hauptschlüssel

Die Zahl in Klammern hinter dem Artnamen ist die jeweils zugehörige Abbildungsnummer.

1. Horn kurz (Verhältnis Horn- zu Afterklappenlänge [H/A] ≤ 1), höchstens so lang wie in Abb. 1d **2**
1'. Horn lang (H/A > 1), mindestens so lang wie in Abb. 2c **14**

2. Kopf, Brustbeine und Horn verdunkelt, oft schwarz (vergl. Abb. 5c) **3**
2'. zumindest der Kopf hell **6**

3. frisch geschlüpft einfarbig schwarz ; nach Nahrungsaufnahme oder im Durchlicht dunkel- bis mittelgrün .... *H. euphorbiae* (5e)
3'. anders **4**

4. Kopf wie lackglänzend, klar in schwarze und bräunliche Partien gegliedert ; Horn an der Spitze deutlich gegabelt ; auf Nadelhölzern .... *H. pinastri* (1d)
4'. anders ; nicht auf Nadelhölzern **5**

5. Kopf und Nackenschild einfarbig schwarzbraun ..... *H. centralasiae* (5d)
5'. Kopf scheckig, nicht einfarbig ; Nackenschild hell .... *H. lineata* (5c)

6. Horn hell oder reduziert **7**
6'. Horn dunkel, normal ausgebildet **11**

7. Horn klein, aber normal ausgebildet (vergl. Abb. 4f) **8**
7'. Horn fast oder ganz zurückgebildet **9**

8. mit langen, schwarzen, Y-förmigen Borsten .... *H. tityus* (3c)
8'. mit hellen, kurzen Borsten .... *H. gallii* (4f)

9. Borsten hell .... *P. proserpina* (4c)
9'. Borsten schwarz **10**

10. Basalfelder der Borsten ebenfalls schwarz .... *H. vespertilio* (4e)
10'. Basalfelder der Borsten hell .... *D. porcellus* (4d)

11. Borsten lang, etwa halb so lang wie das Horn **12**
11'. Borsten viel kürzer **13**

12. Brustbeine dunkel, Horn nur mit den üblichen 2 kräftigen Endborsten........ *M. stellatarum* (4a)
12'. Brustbeine hell, Horn mit 4 kräftigen Borsten .... *R. komarovi* (4b)

13. Kopf und stärker sklerotisierte Teile einfarbig hell ; auf Euphorbiaceae .... *H. nicaea* (5a)
13'. Kopf mit bräunlicher Scheckung ; stärker sklerotisierte Teile (z.B. Bauchbeinschienen) oft dunkel gerandet ; auf Zygophyllaceae .... *H. zygophylli* (5b)

14. Nachschieber nach hinten spitz ausgezogen (vergl. Abb. 2a) **15**
14'. Nachschieber hinten abgerundet **18**

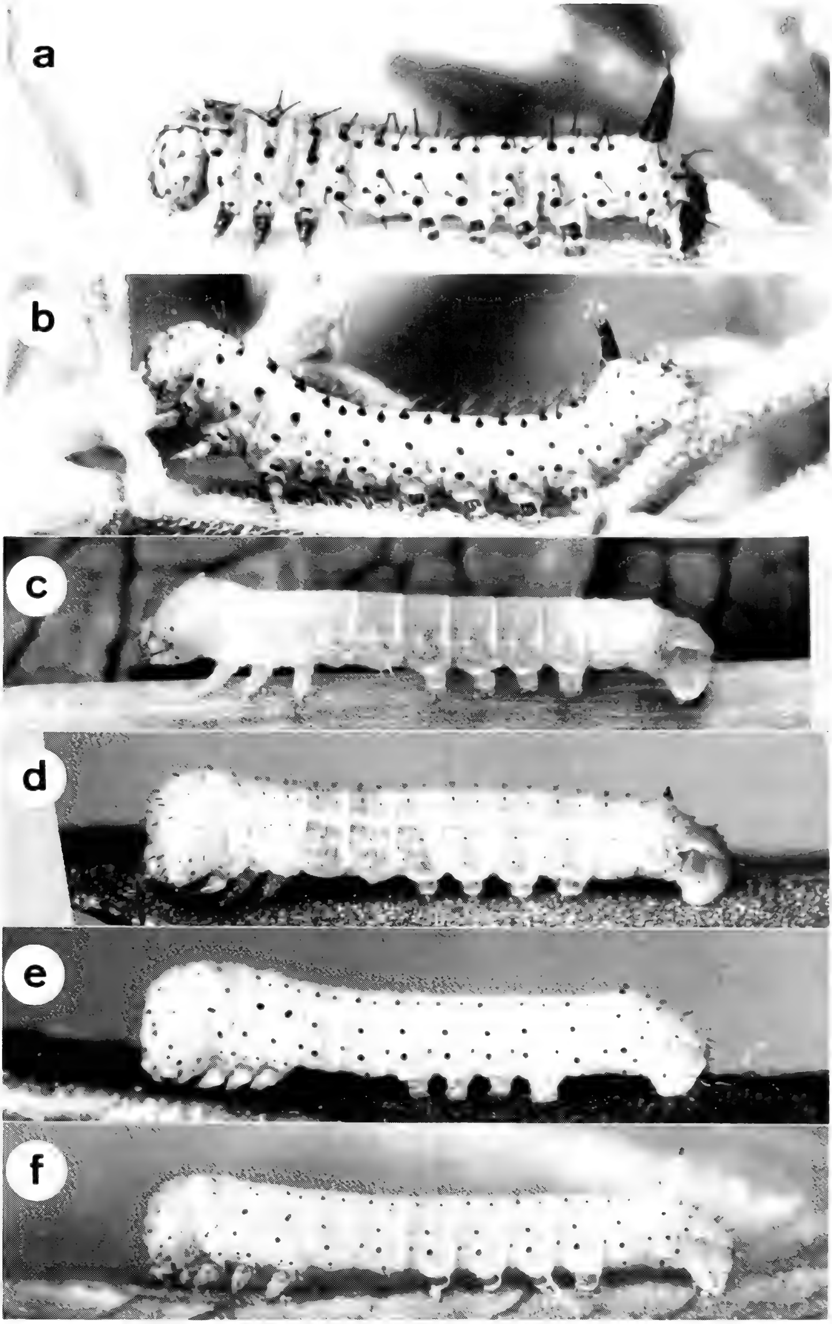

Abb. 4. a) *M. stellatarum* (24 ×) ; b) *R. komarovi* (15 ×, Foto Wasserthal) ; c) *P. proserpina* (26 ×) ; d) *D. porcellus* (19 ×) ; e) *H. vespertilio* (23 ×) ; f) *H. gallii* (23 ×).

15. Horn wie mit schwarzbraunem Hagelzucker bestreut; Prothorax ragt kapuzenartig über den Kopf hinaus ... *M. quercus* (2a)
15'. anders ... **16**

16. Horn über den größten Teil der Länge mittel- bis dunkelbraun ... *S. ocellatus* (2e)
16'. Horn von heller Grundfarbe ... **17**

17. Horn relativ kurz ($H/A < 1,5$), fast glatt ... *L. amurensis* (2c)
17'. Horn lang ($H/A > 1,5$), durch viele kleine Borsten deutlich aufgerauht ... *L. populi* (2d)

18. Körper mit langen, hellen, Y-förmigen Borsten (Abb. 3a-b) ... **19**
18'. ohne solche Borsten ... **20**

19. Borsten auch auf Nackenschild und Kopf tief gegabelt; auf Dipsacaceae ... *H. croatica* (3b)
19'. Nackenschild und Kopf mit einfachen oder nur ganz leicht gegabelten Borsten; auf Caprifoliaceae ... *H. fuciformis* (3a)

20. Körper mit dunklen Borsten auf ebenfalls dunklen Basalfeldern ... **21**
20'. Basalfelder der Borsten hell ... **22**

21. auch Kopf mit schwarzen Borsten ... *H. hippophaes* (6a)
21'. Kopf mit hellen Borsten ... *A. convolvuli* (1b)

22. Horn extrem lang ($H/A \approx 6$!), sehr beweglich ... *H. celerio* (6c)
22'. Horn kürzer ($H/A \leq 4$) ... **23**

23. Raupe durch zusätzliche Kleinborsten (Sekundärborsten; besonders im Gegenlicht gut zu sehen) sehr rauh wirkend ... *M. tiliae* (2b)
23'. nur mit einem einfachen Borstenmuster (vergl. Abb. 1b) ... **24** und **Hilfsschlüssel**

Anmerkung: Lebende Eilarven der folgenden 5 Arten sind bei Lupenvergrößerung nur schwer zu bestimmen; die Futterpflanze der Raupe gibt jedoch oft wichtige Hinweise.

24. Horn relativ kurz und dick ($H/A \approx 2,5$), unbeweglich ... *D. elpenor* (6b)
24'. Horn länger ($H/A \approx 4$) ... **25**

25. Kopfborsten dunkler als Kopf ... **26**
25'. Kopfborsten so hell wie oder heller als Kopf ... **27**

26. Horn dunkelbraun; auf Oleaceae ... *S. ligustri* (1c)
26'. Horn schwarz; auf Vitaceae (u.a.), nicht auf Oleaceae ... *T. alecto* (6d)

27. auf Apocynaceae; Horn äußerst beweglich ... *D. nerii* (3d)
27'. nicht auf Apocynaceae; Horn praktisch unbeweglich ... **28**

28. auf Solanaceae, Oleaceae (u.a.) ... *A. atropos* (1a)
28'. auf Vitaceae, Onagraceae (u.a. ?) ... *T. alecto* (6d)

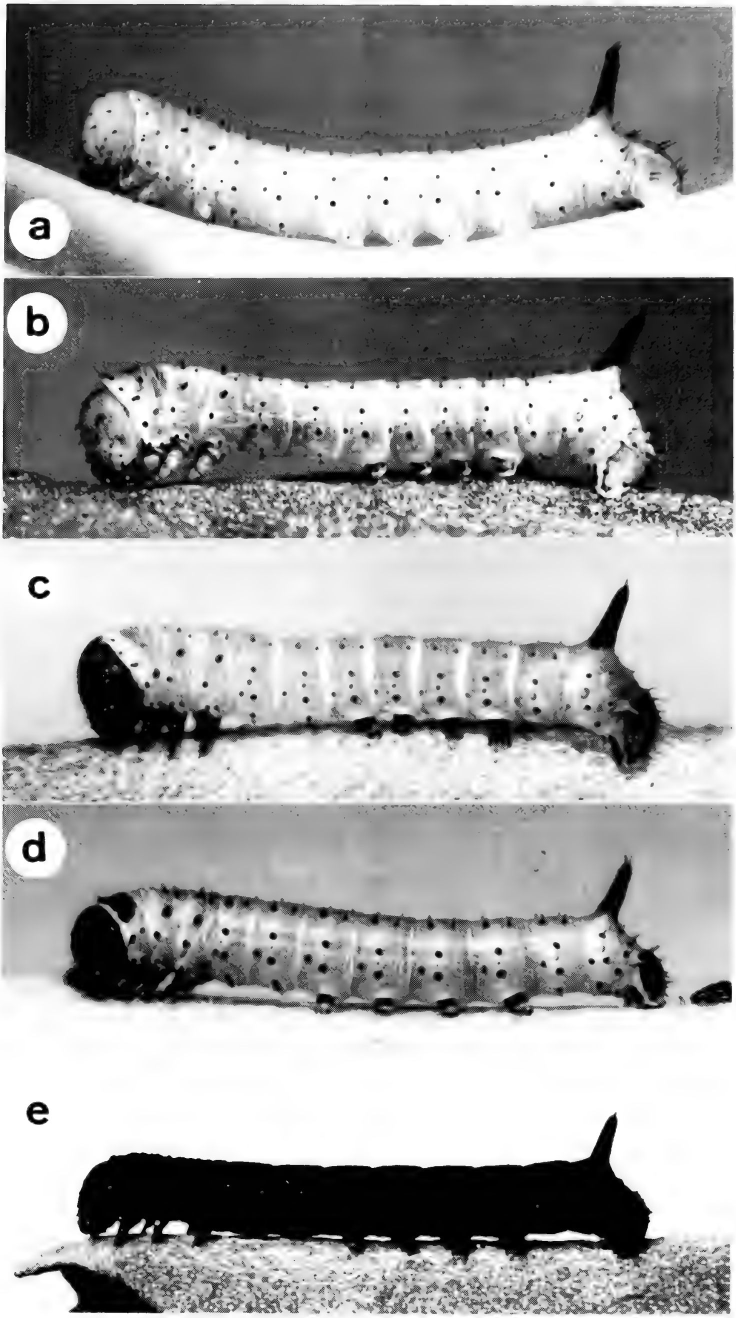

Abb. 5. a) *H. nicaea* (16 ×) ; b) *H. zygophylli* (18 ×) ; c) *H. lineata* (24 ×) ; d) *H. centralasiae* (19 ×) ; e) *H. euphorbiae* (15 ×).

Hilfsschlüssel : 2. Raupenstadium

Lebende Eilarven der Arten *A. atropos, S. ligustri, D. nerii, D. elpenor* und *T. alecto* sind bei Lupenvergrößerung nur schwer zu bestimmen. Dieser Hilfsschlüssel verwendet daher zusätzlich Merkmale des zweiten Raupenstadiums.

1. Körper glatt, mit subdorsalen, paarigen Augenflecken **2**
1'. Körper durch Chitinzapfen aufgerauht, ohne Augenflecken **4**

2. mit einem Augenfleck (Metathorax) .... *D. nerii*
2'. mit mindestens zwei subdorsalen Augenflecken **3**

3. mit zwei subdorsalen Augenflecken .... *D. elpenor*
3'. mit mindestens drei subdorsalen Augenflecken .... *T. alecto*

4. lateral mit deutlichen Diagonalstreifen (von vorn/unten nach hinten/oben) .... *S. ligustri*
4'. ohne Diagonalstreifen .... *A. atropos*

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Mein Dank gilt wiederum Herrn Prof. Dr. L.T. Wasserthal (Erlangen) für technische und wissenschaftliche Anregungen, Herrn Dr. E.A. Loeliger (Oegstgeest [NL]) für Lebendmaterial zahlreicher Arten, Frau I. Paas (Bochum) für die fotografischen Abzüge und Herrn E. de Bros (Binningen [CH]) für die französische Übersetzung der Zusammenfassung.

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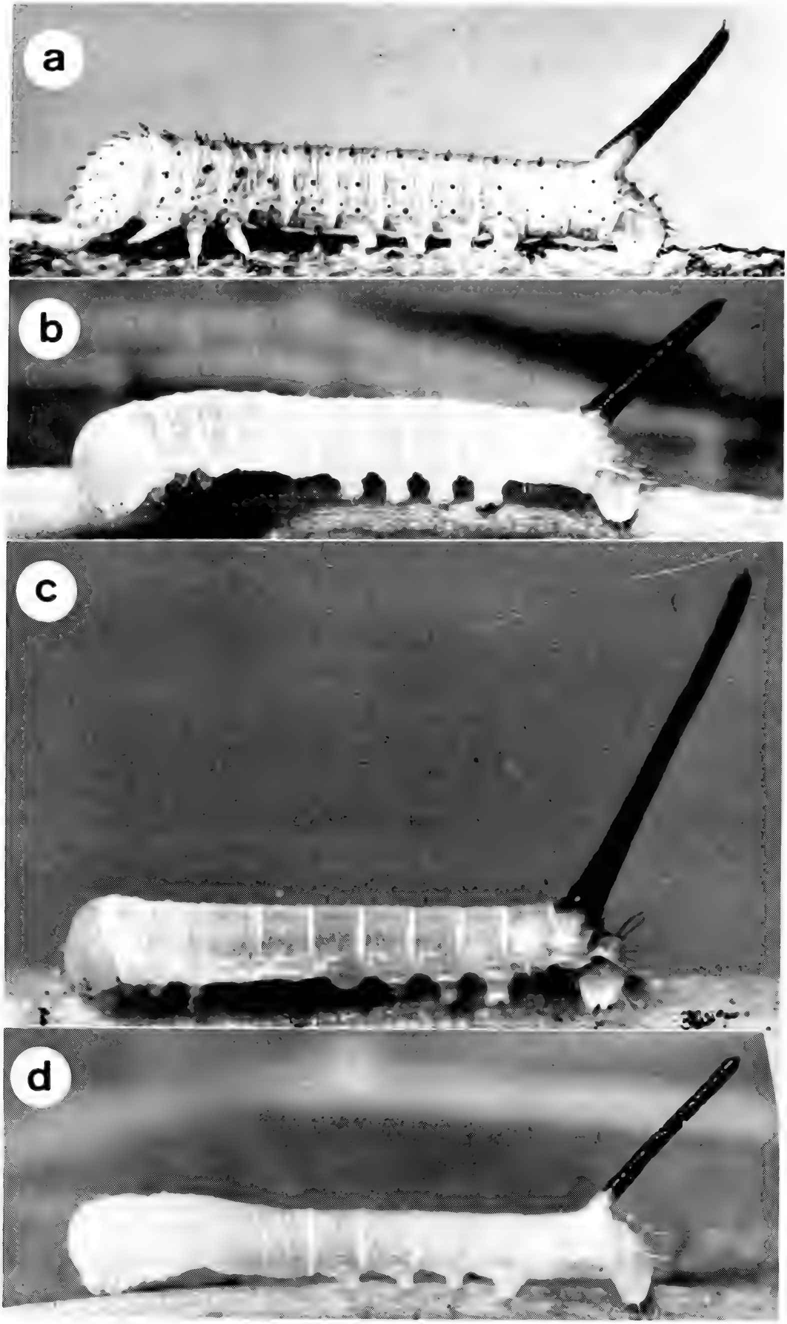

Abb. 6. a) *H. hippophaes* (17 ×) ; b) *D. elpenor* (18 ×) ; c) *H. celerio* (15 ×) ; d) *T. alecto* (14 ×).

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Wing pattern and allozyme relationships in the *Coenonympha arcania* group, emphasising the *C. gardetta-darwiniana* contact area at Bellwald, Switzerland (Lepidoptera, Satyridae)

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Summary

The butterflies *Coenonympha gardetta*, *C. darwiniana* and *C. arcania* are closely related and have parapatric distributions. We studied wing pattern and allozyme variation in three sample sites near Bellwald in Canton Valais, Switzerland in an area where *C. gardetta* and *C. darwiniana* meet, and in a *C. arcania* population from northern Italy. Principal component analysis identified traits that separated the *C. arcania* population, but separate taxonomic groups could not be distinguished in the Bellwald region even when *C. arcania* was dropped from the analysis. Allozyme data showed high polymorphism characteristic of other *Coenonympha* populations, and also separated the *C. arcania* population. F-statistics revealed that the sampled populations at Bellwald, even though separated by up to 2 km, are probably subsites within a single large, demographic population. We believe *C. gardetta* and *C. darwiniana* should be considered conspecific ; *C. gardetta* is the older name. *C. arcania* should provisionally be kept distinct taxonomically, but closer study of contact regions between *C. gardetta* and *C. arcania* are required to rule out mere isolation by distance as the reason for the observed level of differentiation.

Résumé

Coenonympha gardetta, *C. darwiniana* et *C. arcania* sont des espèces proches parentes dont la répartition est parapatrique. Les auteurs ont étudié le dessin des ailes et la variation allozyme de trois lots provenant des environs de Bellwald (Valais, Suisse), région où *C. gardetta* et *C. darwiniana* sont en contact, ainsi que chez une population de *C. arcania* d'Italie septentrionale. L'analyse des principaux éléments a révélé des caractères qui séparaient la population de *C. arcania*, mais on n'a pas du distinguer de groupes taxonomiques séparés dans les biotopes de Bellwald, même lorsque *C. arcania*

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était exclu de l'analyse. Les données allozymes ont révélé un polymorphisme considérable caractéristique d'autres populations de *Coenonympha* ; elles ont également séparé la population de *C. arcania*. Les statistiques F ont prouvé que les populations-échantillons de Bellwald, même séparées par une distance de 2 km, sont probablement des sous-stations à l'intérieur d'une seule et même grande population. Les auteurs pensent que *C. gardetta* et *C. darwiniana* devraient être considérées comme co-spécifiques ; *C. gardetta* est le plus ancien nom. *C. arcania* devrait être provisoirement conservé comme espèce taxonomiquement distincte. Mais on devrait étudier de plus près les zones de contact potentiel entre *C. gardetta* et *C. arcania* afin de pouvoir exclure une simple isolation par la distance pour expliquer le degré de différenciation qu'on a constaté.

Introduction

The butterfly taxa *Coenonympha gardetta* (de Prunner, 1798), *C. darwiniana* Staudinger, 1871 and *C. arcania* (Linnaeus, 1761) are parapatric in the Alps, respectively occupying high (≥ 1800 m), middle (800-2000 m), and low (≤ 1000 m) elevational bands. These taxa have long been seen as closely related (e.g. DAVENPORT, 1941). *C. gardetta* and *C. darwiniana* have contact areas where they are reported to intergrade in the southern Alps (Lepidopterologische Arbeitsgruppe der Schweiz, 1987), leading to questions about their taxonomic status as separate species. Because *C. arcania* is also parapatric, and *darwiniana* is sometimes listed in its synonomy (e.g. FORSTER & WOHLFAHRT, 1976), it is legitimate to question the relationships among all three taxa.

In this study, we examine three populations at the contact zone between *Coenonympha gardetta* and *C. darwiniana*, and a geographically distant population of *C. arcania*. If there is indeed partial (or complete) genetic isolation between these taxa, as the current taxonomy suggests, then our contact populations should contain an excess of "pure" forms of each taxon, and few intermediates. Upon closer statistical examination, suites of diagnostic wing pattern and/or allozyme traits would appear to be correlated within individuals in these populations. However, if the major diagnostic differences between these taxa are produced by environmental conditions operating on a common genotypic array rather than by genetic differences maintained by "reproductive" barriers, then there should be no such correlations within contact populations. A similar lack of correlation would result in contact areas if hybrids between immigrants from taxonomically differentiated regional populations were not at a selective disadvantage relative to "pure" individuals. Furthermore, for traits inherited in a co-dominant Mendelian fashion (allozymes in this study), such correlations can also be expressed in the form of F-statistics (WRIGHT, 1969). These have the advantage of permitting us to enlist the analytical power of evolutionary theory to make inferences about underlying populational processes, in particular gene exchange among populations. Of course, it is gene exchange between putative taxonomic groupings that we wish to infer in the process of making taxonomic decisions. Taxonomists have traditionally done this "by eye" and therefore less reliably, especially for the traits whose genetic bases are unknown.

Methods

Mixed populations of *Coenonympha gardetta* and *C. darwiniana* were sampled in July 1991 in the vicinity of Bellwald, Switzerland, on the north slope of Canton Valais in the Rhone Valley. Population I was collected on a steep, SW-facing slope at 1700m in a meadow under an open-canopy fir forest on 13.vii.1991. Population II was sampled also at 1700 m, but 1 km N on a NW-facing, colder slope, locally above treeline, on 20.vii.1991. Population III was at 2000 m at the top of the ski lift, above the treeline in open meadow, on 21.vii.1991. The *C. arcania* population was collected at 1400 m from Monte Mottarone, near Streza, Italy, on 23.vii.1991. Individuals were haphazardly netted and stored alive under refrigeration until they could be frozen at -80C.

Wing pattern morphometrics

The taxonomic literature (DAVENPORT, 1941 ; HIGGINS & HARGREAVES, 1991 ; Lepidopterologische Arbeitsgruppe der Schweiz, 1987) was consulted to determine the wing pattern elements previously used to distinguish the three taxa, especially between the more similar taxa, *gardetta* and *darwiniana*. The characters proved to be mainly the size and location (relative to the wing margin) of the eyespots in the distal wing cells of the ventral hindwing, and the extent and location of the white band proximal to these spots. Spots near the apex of the ventral forewing have also been used.

Wings were removed and stored separately when specimens were prepared for electrophoresis (described below). We measured the following characters for each of eight ventral hindwing cells, along the axis of the cell : the diameter of the black center of the eyespot (absent = 0), the distance from the center of the eyespot to the wing margin (absent = unscored), the width of the white band measured to the edge of the eyespot halo (absent = 0), and the edge of the white band to the edge of the wing (absent = unscored). We also measured the diameter of the forewing eyespots (absent = 0). We did not record from the outer wing spot rings because yellow outer rings could not be consistently distinguished when the ground colour was pale ; our scoring system thus regarded any all-yellow spots as being absent. Wing length was measured as an index of body size, and gender was recorded. The left wings were used except when one or more characters was missing due to damage, whereupon the right wings were used. Measurements were made at 20x magnification on a colour video monitor using a computerised image-analysis system. A Wild® microscope was fitted with a Sony® video camera ; this was connected to IBM PC® computer operated using the image-analysis program Optimas® (v. 3.01, BioScan, Inc.). Data collection was mechanised using a macro written in the Optimas procedural language, and measurements were saved directly to a file. We avoided characters involving colour because they were not amenable to accurate measurement using this software.

We analyzed the wing patterns using principal component analysis. This method condenses the large number of measurements per individual into a more manageable number of statistically independent characters, and is justifiable both statistically and biologically. The premise, statistically, is that some characters are likely to be correlated, whereupon they carry redundant information and should be weighted to take this into account. For example, large individuals are likely have larger measurements, and we should factor out the body size differences before we attempt to consider relative eyespot size differences. Biologically, the premise is that if the taxa are genetically isolated, then their wing patterns will have evolved independently in the separate lineages, and different pattern elements will be correlated, within lineages. The elements that are correlated would form the set of diagnostic characters useful for distinguishing the lineages. If genetic isolation were indeed involved, a small number of principal components would contain all the correlated diagnostic characters and describe most of the overall wing pattern variation among individuals, even within contact areas. But if the taxa were freely interbreeding, then characters in contact areas would tend to be assorted independently among individuals ; they would be uncorrelated. Statistically, this would be indicated if the overall wing pattern variation were spread among a larger number of principal components, evidence of independence among the wing pattern elements, and by unimodal variation along principal component axes.

Principal components analysis is, in its philosophy, what the experienced taxonomists of older generations did "by eye". The advantages of the statistical approach are three. Firstly, it is explicit, thus repeatable by others and carries known data limitations. Secondly, it is grounded in statistical theory so it takes sample size into account in a way that cannot be done properly otherwise. Finally, it can pick out much more subtle patterns than can the eye of an experienced worker, and conversely, it can demonstrate that some patterns perceived by less experienced eyes are fantasy. However, both approaches depend on the ability to pick out the "right" characters to measure, those that will give the best discrimination ; this is why, for characters in this study, we relied on the literature for the acknowledged expertise of previous workers.

We used Systat® (v.5.1, Systat Inc.) software on a Macintosh computer for the principal components analysis. We used a Pearson's r correlation matrix of the 28 primary measurements/individual to generate all principal components (PCs) ; gender and body size were included in these analyses as controls. The statistics require data sets without missing entries, so we were forced to omit the measures of spot or white line location for some wing cells if any individuals were absent that trait (the rejected alternative was to eliminate those individuals). We examined the loadings of characters onto each PC for suites of diagnostic characters. The proportion of the total wing pattern variance explained by each PC was used as an estimate of the overall independence of traits. We then analyzed the corresponding PC scores of each individual (i.e., the "measurement" of the individual along the PC axis, produced as a weighted combination of the original measurements in that individual) using one-way ANOVAs for to find significant variation among populations, using SuperANOVA® (v4.0 ; Abacus Concepts, Inc.) software on a Macintosh computer. The entire analysis was repeated without the *C. arcania* population to look more closely at differentiation in the Bellwald region ; here we could use a larger data set because fewer individuals were absent the eyespots or white lines in cells.

Electrophoresis

Horizontal starch gel electrophoresis was performed on head and thorax tissue using standard methods described elsewhere (PORTER & GEIGER, 1988 ; PORTER & MATOON, 1989). We scored 19 putative genetic loci : alcohol dehydrogenase (ADH ; enzyme commission number 1.1.1.1), adenylate kinase (AK-1 ; 2.7.4.7), aldolase (ALDO ;

4.1.2.13), esterase (EST-1 ; 3.1.1.1), fumarase (FUM ; 4.2.1.2), glutamic-oxaloacetic transaminase (GOT-1, GOT-2 ; 2.6.1.1), glyceraldehyde-3-phosphate dehydrogenase (GAPDH ; 1.2.1.12), α-glycerophosphate dehydrogenase (αGPDH ; 1.1.1.8), hexokinase (HK ; 2.7.1.1), isocitric dehydrogenase (IDH-1 ; 1.1.1.42), lactic dehydrogenase (LDH ; 1.1.1.27), malic dehydrogenase (MDH-1, MDH-2 ; 1.1.1.37) , malic enzyme (ME-1, ME-2 ; 1.1.1.40), peptidase (PEP-1 ; 3.4.1.1), phosphoglucomutase (PGM ; 2.7.5.1) and phosphoglucose isomerase (PGI ; 5.3.1.9).

We calculated standard statistics describing the extent of allozyme variability within populations. These include the mean number of alleles observed per locus, the mean heterozygosity observed per locus (H_{obs}) and that expected based on Hardy-Weinberg expectation (H_{exp}), and the percent of sampled loci that were polymorphic in the population (%P).

We describe variation among populations in two ways. First, we calculated Nei's unbiased genetic distance and produced a summary phenogram using UPGMA. This method is probably most familiar and permits comparison across a wide range of taxa. We also estimated F_{ST} (WRIGHT, 1969) among the Bellwald populations using WEIR & COCKERHAM's (1984) method which accounts for sampling variation. We used weighted averaging over alleles and loci, and jackknifed over loci for the error estimates. Our estimates were interpreted using the relationship $M \approx (1/F_{ST}\text{-}1)/4$, where M is a gene flow parameter describing the effective number of individuals moving among populations each generation (COCKERHAM & WEIR, 1993). A fundamental result in theoretical population genetics is that when $M > 0.5$, then gene flow produces substantial genetic similarity among populations at neutral loci (WRIGHT, 1931). We will not provide the theoretical and statistical details here ; interested readers may consult population genetic texts (e.g. HARTL & CLARK, 1989) for introductory concepts, COCKERHAM & WEIR (1993) and references therein for current statistical theory, and PORTER (1990) and PORTER & GEIGER (1988 ; 1995) for examples of applications to butterfly populations.

Results

Wing pattern morphometrics

Coefficients of variation (c.v.) for each trait are shown for each population and for all populations combined (Table 1). A c.v. of 0.1 means that the standard deviation is 10% of the mean for the trait, a reasonably

Table 1

Coefficients of variation for the ventral wing pattern characters used in this study. Missing values indicate the trait was not present in the population

character	Bellwald I	Bellwald II	Bellwald III	Mt. Mottarone	total
n	26	9	35	17	87
forewing length	0.16	0.11	0.14	0.14	0.15
forewing spot diameter					
1	5.00			4.24	8.67
2	1.36	0.80	0.98	0.68	1.00
hindwing spot diameter					
1	0.22	0.19	0.32	0.30	0.33
2	0.29	0.56	0.33	0.70	0.44
3	0.39	0.18	0.22	0.28	0.31
4	0.23	0.13	0.21	0.21	0.29
5	0.21	0.13	0.16	0.37	0.29
6	0.39	0.14	0.40	1.00	0.51
white line width					
1	0.54	0.57	0.51	0.44	0.60
2	0.42	0.50	0.32	0.33	0.41
3	0.39	0.52	0.32	0.26	0.39
4	0.47	0.79	0.55	0.23	0.55
5	0.53	1.01	0.77	0.44	0.63
6	0.49	0.48	0.61	0.59	0.57
7	1.15	0.65	1.31	0.71	1.04
8	3.49		3.02	2.48	3.16
spot location					
1	0.43	0.45	0.54	0.44	0.51
2	0.17	0.09	0.22	0.58	0.30
3	0.16	0.10	0.22	0.18	0.19
4	0.15	0.12	0.17	0.40	0.27
5	0.17	0.08	0.22	0.41	0.28
6	0.37	0.11	0.32	1.07	0.50
white line location					
1	0.41	0.31	0.31	0.53	0.42
2	0.17	0.26	0.16	0.37	0.23
3	0.19	0.29	0.19	0.33	0.27
4	0.18	0.37	0.26	0.41	0.39
5	0.20	0.37	0.26	0.50	0.41
6	0.37	0.21	0.32	0.62	0.48
7	1.03	0.20	0.93	0.65	0.86
8	2.44		2.59	1.53	2.26

high level of variability. Variability is high in the wing pattern traits taxonomists have identified as important, being generally higher than c.v. = 0.2, and is comparable among populations. Some traits, particularly those present in only a few individuals, showed c.v. > 1, an extreme level of variability. This included pattern elements in hindwing cells 7 and 8, and in the forewing spots.

First consider variation in all populations. Eigenvalues and the proportion of total variance explained by the first ten PCs are in Table 2. The character loadings of the first six PCs are given in Table 3. PC 1 loaded highly for most characters, especially for forewing length, and we interpret it as a general body size character. Note that several traits did not load here, indicating that these varied relatively independently of body size (this points out the hazards of an alternative approach : dividing all measurements by body size for standardisation before statistical analysis). These include the spot diameter in cell 6 and the white line width in cell 1. PC 2 describes an inverse ratio of spot diameter and white line width, and is largely independent of body size. PC 3 mainly describes the shape of the white line as it traverses the cells, with loadings being positive in the first cells and negative in the later cells ; the spot diameters in cells 2 and 6 and the width in cell 2 also load here. This PC captures a previously reported taxonomic difference between *arcania*, with a line that narrows posteriorly, and the others, with a line of relatively constant width. PCs 4 and 5 describe subtle relationships between spot diameters, white line widths and their locations in several cells. PC 6 describes sexual dimorphism, and characters that also load here include the spot diameter of cell 6 and the white line width in cell 8.

Table 2

Principal component analysis with all population included.
Eigenvalues of the first ten PCs
and the percent of the total variance explained

PC	Eigenvalue	% variance explained
1	5.860	29.3
2	3.101	15.5
3	2.203	11.0
4	1.442	7.2
5	1.437	7.2
6	1.313	6.6
7	1.086	5.4
8	0.578	2.9
9	0.567	2.8
10	0.407	2.0

Figure 1 shows differentiation among populations in PC scores. We found significant interpopulational differences in PC 1 (ANOVA ; $F_{3,72} = 14.958$; $P < 0.0001$), with two groups segregating in the followup test (Duncan's New Multiple Range Test, $P < 0.05$) : the

Table 3

Character loadings on the first six principle components using all populations.
Numbers for traits refer to wing cells.
Loadings are the extent to which a character is correlated with the PC

trait	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
gender	0.020	-0.249	0.076	-0.079	0.262	-0.843
forewing length	0.824	0.092	0.283	-0.133	-0.150	-0.018
forewing spot diameter						
2	0.313	0.317	-0.236	0.021	0.230	-0.122
hindwing spot diameter						
1	0.729	0.408	-0.160	-0.115	0.084	0.204
2	0.256	0.304	0.389	0.521	0.366	-0.141
3	0.516	0.486	0.086	0.070	0.519	0.091
4	0.782	0.411	-0.223	-0.043	0.145	0.018
5	0.684	0.321	-0.203	0.243	0.061	0.053
6	0.040	0.053	0.402	0.534	-0.407	0.356
white line width						
1	0.072	-0.305	0.772	-0.172	0.374	-0.010
2	0.340	-0.596	0.501	-0.119	0.052	0.146
3	0.617	-0.561	-0.111	-0.339	-0.060	0.077
4	0.495	-0.435	-0.535	-0.232	0.119	0.154
5	0.411	-0.710	-0.055	0.090	0.163	0.213
6	0.479	-0.547	0.043	0.331	0.254	0.143
7	0.565	-0.394	-0.253	0.330	0.055	-0.084
8	0.200	-0.392	-0.210	0.480	-0.313	-0.430
indwing spot location						
3	0.797	0.012	0.077	0.090	-0.401	-0.118
white line location						
2	0.555	0.244	0.600	-0.255	-0.277	-0.130
3	0.832	0.189	0.010	-0.199	-0.321	-0.221

Mottarone and Bellwald II population both had larger mean body sizes than the other populations (Figure 1a). The Mottarone population (*arcania*) differed from the others in PC 3 (ANOVA ; $F_{3,72} = 17.164$; $P < 0.0001$), indicating a difference in white line shape between these groups (Figure 1b). PC 6 also showed significance (ANOVA ; $F_{3,72} = 3.233$; $P = 0.027$), but we attribute this to a difference in sex ratios among populations. These differences demonstrate that the *arcania* population is phenotypically different from the remaining populations, and by themselves, suggest a possibility of genetic isolation. Means of PCs 2, 4 & 5 were not significantly different among populations, and we consider them to represent patterns of variation common to all populations.

The differences between *arcania* vs. Bellwald populations could potentially obscure more subtle differentiation between *gardetta* and *darwiniana* in the contact zone, so it is appropriate to reanalyze the data dropping the Mottarone population.

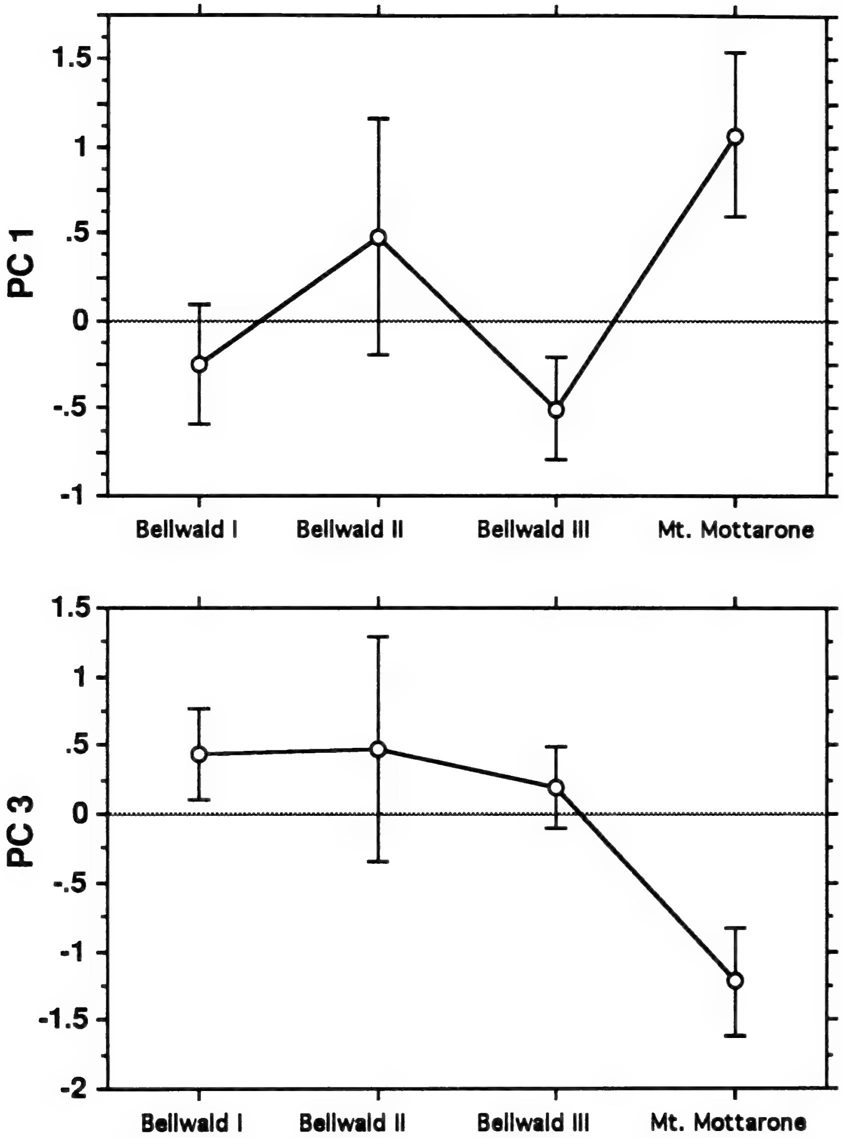

Fig. 1. Principal component means (95% c.i.) showing differences among populations. (a) PC 1, describing body size ; (b) PC 3, describing the shape of the white line.

Table 4

Principal component analysis with only Bellwald populations. Eigenvalues of the first ten PCs and the percent of the total variance explained

PC	Eigenvalue	% variance explained
1	8.718	36.3
2	3.946	16.4
3	2.322	9.7
4	1.701	7.1
5	1.507	6.3
6	1.038	4.3
7	0.740	3.1
8	0.648	2.7
9	0.616	2.6
10	0.514	2.1

Here we concentrate on the *gardetta/darwiniana* sampling sites at Bellwald, excluding *arcania.* Eigenvalues and the proportion of total variance explained by the first ten PCs are in Table 4. The character loadings of the first six PCs are given in Table 5 ; it is important to remember that these PCs describe different combinations of characters than those in the previous analysis. PC 1 again loaded highly for most characters, especially for forewing length, and we interpret it again as a general body size character. The forewing spot diameter and the several of the white line widths vary little with body size, nor is there sexual size dimorphism. PC 2 shows strong negative loadings for white line width and weak positive loadings for spot diameters. We interpret it as a white line width parameter that is in relative agreement with a diagnostic character often used to separate *gardetta* and *darwiniana.* PC 3 describes a differentiation pattern in inter-cell ratios of spot and white line sizes — at one extreme are *darwiniana*-like individuals with the middle cells having relatively smaller spots and extreme cells having wider lines, at the other are individuals with the reverse. PC 4 describes sexual dimorphism, with hindwing spot 6 being larger in males and the white band slightly more centrally located in females. PCs 5 & 6 describe mainly relationships among spot sizes.

We found significant differences among populations only in PC 4 (ANOVA ; $F_{2,57} = 5.093$; $P = 0.009$), and this was attributed to the different sex ratios of these population samples. The difference in body size from the previous analysis was not quite significant here (ANOVA ; $F_{2,57} = 2.736$; $P = 0.073$). Distributions for all three Bellwald populations along PC axes 2 & 3 are shown in Figure 2 ; these axes describe

Table 5

Loadings for the first six PCs for the *gardetta-darwiniana* contact area only

trait	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
gender	-0.009	-0.256	0.053	-0.758	0.336	-0.173
forewing length	0.870	0.003	0.084	-0.007	-0.219	0.063
forewing spot diameter						
2	0.169	0.232	0.208	0.002	0.657	-0.569
hindwing spot diameter						
1	0.630	0.271	0.260	0.229	-0.033	0.177
2	0.445	0.276	0.308	-0.299	0.368	0.358
3	0.451	0.267	0.653	0.035	0.202	0.200
4	0.801	0.233	0.310	0.147	0.215	0.035
5	0.771	0.156	0.005	0.283	0.294	0.090
6	0.447	0.092	-0.441	0.583	0.268	-0.084
white line width						
1	0.383	-0.288	0.610	-0.260	-0.212	-0.219
2	0.541	-0.643	0.230	-0.011	-0.129	-0.156
3	0.298	-0.812	0.079	-0.030	-0.205	-0.077
4	-0.087	-0.794	0.111	0.291	0.128	-0.240
5	0.189	-0.795	0.120	0.136	-0.018	0.156
6	0.312	-0.641	0.184	0.093	0.166	0.365
7	0.318	-0.591	-0.074	0.039	0.367	0.033
8	0.048	-0.468	-0.597	-0.310	0.313	0.332
hindwing spot location						
2	0.869	0.055	-0.220	0.042	-0.105	-0.196
3	0.847	-0.094	-0.372	0.034	0.038	-0.112
4	0.863	0.053	0.126	0.099	-0.218	0.004
5	0.850	-0.067	-0.287	0.021	-0.139	-0.078
white line location						
2	0.808	0.257	0.042	-0.261	-0.258	-0.057
3	0.853	0.135	-0.253	-0.328	-0.074	-0.017
5	0.780	0.135	-0.430	-0.274	0.012	0.012

most of the *gardetta-darwiniana* diagnostic characters. Despite the numerous individuals that appear to have *gardetta* and *darwiniana* characteristics, there is unimodal variation and no evidence from wing pattern that these taxa are genetically isolated.

Allozyme differentiation

Allelic frequencies for variable loci are given in Table 6. The loci EST-1, GAPDH and αGPDH were monomorphic. Summary statistics describing genetic variability within populations is given in Table 7. Variability is remarkably high, a common phenomenon in butterfly populations, including *Coenonympha* (PORTER & GEIGER, 1988 ; PORTER & MATOON, 1989), and indicates that these populations are quite large and have not been through population bottlenecks in their recent past.

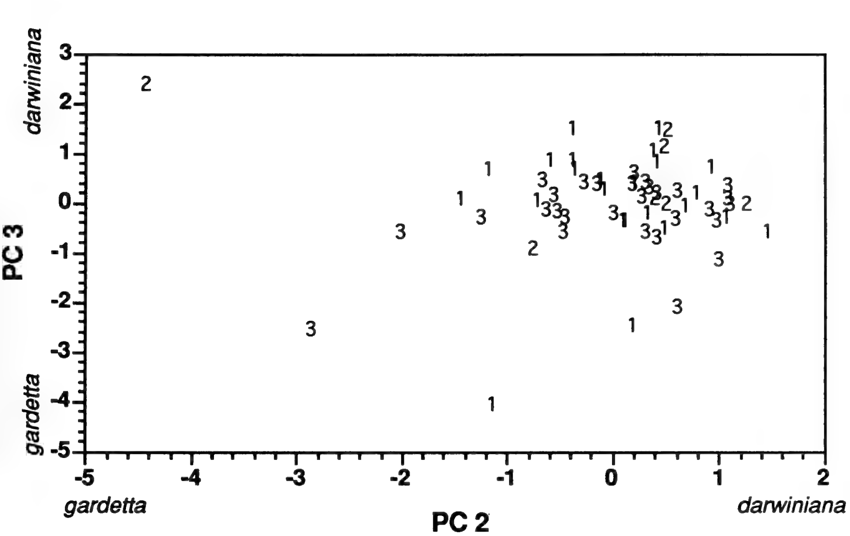

Fig. 2. Distributions of individuals from the Bellwald populations along PC axes 2 & 3 are unimodal. 1 — from Bellwald I; 2 — Bellwald II; 3 — Bellwald III. PCs are standardised to have their means at zero and scale in units of standard deviations. The populations do not differ significantly along either axis.

Differentiation among populations is described graphically using a distance Wagner procedure (Farris, 1972) on a matrix of pairwise Rogers' (1972) genetic distances (Figure 3a), and using UPGMA cluster analysis on a matrix of Nei's (1978) unbiased genetic identities (Figure 3b). The Mottarone *arcania* population segregates from the others, at a level suggesting that it may be genetically isolated. The remainder cluster closely, at levels commonly observed among conspecific populations in other butterfly taxa.

The high similarity within the Bellwald group permits closer populational analyses using F-statistics. Within the Bellwald population group, we obtained an estimate of θ ($= \hat{F}_{ST}$) $= - 0.00223 \pm 0.00127$ (s.d.), averaged over alleles and loci. This slightly negative value is a result of sampling error and shows that θ is not significantly different from zero, indicating that there is no appreciable genetic differentiation among sites. This is perhaps more easily understood when translated to a gene flow estimate ($\hat{M}$) using $\hat{M} = (1/\theta - 1)/4$, yielding a value of $942 \leq \hat{M} \leq$ panmictic (95% c.i.). This large number of individuals exchanged among sites each generation suggests that the sampled "populations" are effectively sub-sites within a single, larger panmictic population in the Bellwald area.

Table 6

Allele frequencies for variable loci, by population.
Sample sizes for each locus in brackets

	Monte Mottarone	Bellwald I	Bellwald II	Bellwald III
FUM	[17]	[23]	[9]	[31]
A	0.029	0.065	0.111	0.016
B	0.676	0.674	0.778	0.774
C	0.294	0.261	0.111	0.210
GOT-1	[17]	[26]	[9]	[34]
B	0.118	0.135	0.278	0.074
C				0.044
D	0.118	0.731	0.611	0.691
F	0.471	0.038		0.029
G		0.058	0.056	0.118
H	0.294	0.038		
I			0.056	0.044
GOT-2	[10]	[14]	[8]	[16]
A		0.071	0.312	0.156
B	1.000	0.929	0.688	0.844
HK	[18]	[26]	[9]	[35]
A	0.028			
B	0.972	1.000	1.000	1.000
IDH-1	[16]	[26]	[9]	[34]
A	0.969	1.000	1.000	1.000
C	0.031			
LDH	[6]	[21]	[7]	[25]
A	1.000			
B		0.238	0.500	0.360
D		0.762	0.500	0.640
MDH-1	[17]	[26]	[9]	[35]
A	0.029	0.404	0.500	0.371
B	0.971	0.596	0.500	0.629
MDH-2	[18]	[26]	[9]	[35]
A	1.000	1.000	1.000	0.986
B				0.014
ME-1	[8]	[16]	[9]	[23]
A	1.000	0.969	1.000	1.000
B		0.031		
ME-2	[8]	[16]	[9]	[24]
A	0.062			
B	0.938	1.000	1.000	1.000
PEP-1	[17]	[26]	[9]	[34]
A	0.088	0.058	0.056	0.029
B	0.618	0.635	0.778	0.676
C	0.294	0.308	0.167	0.294
PGI	[18]	[26]	[9]	[35]
B	0.083	0.077	0.111	0.014
C				0.014
D	0.583	0.173	0.167	0.129
E	0.028			
F	0.278	0.615	0.611	0.643
G	0.028	0.019		
H		0.096	0.111	0.143
I		0.019		0.029
J				0.029
PGM	[18]	[26]	[9]	[35]
A	0.111	0.154		0.143
B	0.111			
D	0.417	0.827	0.944	0.800
E	0.361	0.019		0.057
G			0.056	

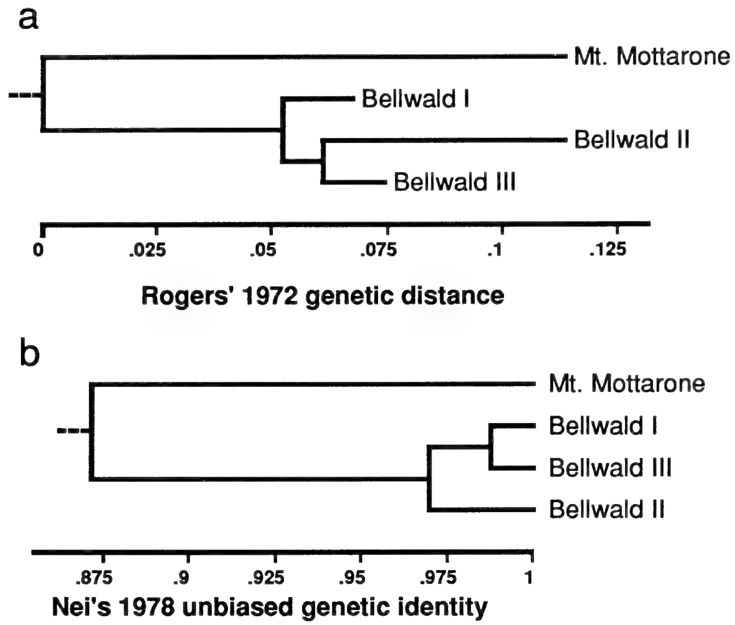

Fig. 3. Genetic differentiation among populations, described by (a) a distance Wagner procedure (Farris, 1972) using Rogers' (1972) genetic distance, rooted using the midpoint of the longest path ; (b) UPGMA using Nei's unbiased genetic identity.

Table 7

Genetic variability within populations (s.e.).
A : mean alleles per locus ; %P : percent of loci that were polymorphic ;
H_{obs} : the observed proportion of heterozygotes, averaged over loci ;
H_{exp} : the proportion of heterozygotes expected from Hardy-Weinberg genotypic proportions, averaged over loci.
Standard errors calculated using a jackknife procedure, over loci

	population	A	%P	H_{obs}	H_{exp}
1	Monte Mottarone	2.27 (0.02)	60.0 (0.9)	0.229 (0.005)	0.199 (0.004)
2	Bellwald I	2.33 (0.03)	60.0 (0.9)	0.187 (0.004)	0.207 (0.004)
3	Bellwald II	2.00 (0.02)	53.3 (0.9)	0.213 (0.004)	0.212 (0.004)
4	Bellwald III	2.47 (0.03)	60.0 (0.9)	0.192 (0.004)	0.213 (0.004)

Discussion

Both morphological and allozyme analyses show that the Monte Mottarone *C. arcania* population is different from the others, but that continuous variation exists between *C. gardetta* and *C. darwiniana* at Bellwald. The morphometric analyses isolated essentially the same suites of "diagnostic" character states that taxonomists have used, showing that the results are not spurious as has been suggested in similar studies (Hammond, 1985). Neither is the high genetic similarity a spurious result of low variability : genetic variability is high enough that if two species have been coexisting at Bellwald, then genetic drift should have already differentiated the populations (see Porter & Geiger, 1995 for a discussion of this effect). There is no evidence to suggest that these are distinct species at Bellwald.

The *C. gardetta-darwiniana* contact region is similar to contact regions between *C. tullia* (Müller, 1764) taxa in western North America. *C. tullia*-group taxa in California, Nevada and Oregon differ in eyespot size and number, dorsal and ventral ground colour and the shape and placement of the white lines, and were distributed among several nominal species. However, populations are highly variable, and taxonomists, with the notable exception of Davenport (1941), had tended concentrate on widely separated localities, ignoring contact areas and intrapopulational variability. When contact areas were examined, and allozyme data used as corroborating evidence, it was found that wing patterns intergraded, gene flow was high, and no genetic isolation was apparent (Porter & Geiger, 1988). Instead, the geographic variation in wing pattern was attributed to unknown selective and/or historical factors, being maintained in the face of strong gene flow between the taxonomically recognised forms. In one remarkable example, a population on coastal dunes was sharply differentiated in wing pattern from one only 8 km away on a hilltop, yet the allozyme data could only be reasonably interpreted as showing evidence of strong gene flow between them (Porter & Matoon, 1989).

The allozyme data indicate that the *C. gardetta-darwiniana* population at Bellwald is probably quite large and demographically continuous over an area of several km^2. This area encompasses the respectively "typical" subalpine and alpine habitats of *C. darwiniana* and *C. gardetta*, and is consistent with the interpretation that no genetic isolation exists between them. The implication is that individuals are quite mobile, readily moving distances of 2 km or more in their lifetimes. Whereas this should obviously be verified with a demographic study, we point out that marked *C. tullia california* Westwood, 1851 in California have been recaptured at distances >1 km (WEISSMAN, 1972), and stray individuals have been seen in the Central Valley (Davis area) at least 40 km from potential source populations (SHAPIRO, 1982; PORTER, pers. obs.).

We believe *C. gardetta* and *C. darwiniana* should be considered conspecific and the younger name, *darwiniana*, be placed in synonymy. This decision is based on the high genetic and phenotypic variability in the contact zone without apparent isolation, and remains subjective pending verification by closer demographic studies there. However, the patterns are strongly suggestive, and the onus now properly belongs on a splitter to demonstrate that *C. gardetta* and *C. darwiniana* are genetically isolated, rather than being extremes of a cline as we believe they are. Indeed, the high gene flow estimate would argue that *darwiniana* not even be used as a subspecies name, because individuals from populations of "*darwiniana*" wing phenotype are likely to be much more closely related in pedigree to those from "*gardetta*" populations directly upslope than to butterflies from populations with "*darwiniana*" phenotypes at more distant localities. A minor difference between *C. gardetta* and *darwiniana* in the male genitalia has been identified (HIGGINS, 1975), but DAVENPORT (1941) found the genitalia to be quite variable. Regardless of the validity of this putative difference, small differences in the genitalia *per se* have little value as evidence of reproductive isolation between parapatric taxa (PORTER & SHAPIRO, 1990).

The possibility also remains that *C. arcania* and *C. gardetta* (+ *darwiniana*) are conspecific, as we have only studied widely separated populations and these taxa too may intergrade in their contact areas. However, both the allozyme and wing pattern differentiation in our limited data are consistent with differences between closely related sympatric taxa, and we believe their continued designation as species — the *status quo* — is appropriate pending publication of studies done in contact areas. Anticipated results from a current study of the *C. arcania* group, on a larger geographic scale than ours (WIEMERS, 1994), will bring us much closer to the solution of this problem.

Systematists of *Coenonympha* have long relied heavily on qualitatively described wing pattern dimensions as characters, even while lamenting their intra- and interpopulational variability (DAVENPORT, 1941). Species-level taxonomic decisions in *Coenonympha* could be greatly illuminated if we understood more about how wing pattern is developmentally, genetically and ecologically controlled, because it would help us determine the extent to which character variation could be used as markers for more profound genetic differentiation. Studies of the wing patterns of *Coenonympha* indicate that several taxa have clines in spot pattern, with spot size diminishing with increasing elevation (Brunton *et al.*, 1991) or latitude (K. Porter, 1980 ; Dennis *et al.*, 1986) ; these patterns also appear to occur in North American *C. tullia* but have not yet been studied quantitatively. Though the eyespots of the Nymphalidae are probably serially homologous (Nijhout, 1991), multivariate statistical analyses have demonstrated that the pattern elements in different wing cells are largely developmentally independent (Nijhout, 1985 ; Dennis *et al.*, 1984). Dennis *et al.*, (1986) proposed that geographic variation in spot size in *C. tullia* is attributable to parallel variation in selection pressures imposed by different suites of predators or predator abilities relative to gross habitat type. The alternative that one might infer from clinal variation, that spot pattern is not genetically controlled at all, seems unlikely given the weaknesses of correlations of spot sizes within individuals and the heritability of spot pattern in other Satyrinae (Brakefield & Noordwijk, 1985). It would also be difficult to credibly explain, without invoking adaptive genetic differences, why spot size gets smaller with increasing elevation in *C. gardetta*, but larger with increasing elevation in *C. corinna* and North American *C. tullia*, even though the ecological causes of these putative adaptations remain elusive. This is not to exclude an important role for environmental effects : polyphenism is apparent in several satyrine taxa, e.g. *Bicyclus* (Brakefield & Reitsma, 1991) and *C. tullia* (Weissman, 1972), indicating the presence of genotype by environment interactions in the control of wing pattern. Though *C. arcania* and *C. gardetta* usually have only a single annual generation, similar underlying genetic mechanisms could well be influencing their wing patterns. Unfortunately, there are substantial technical difficulties to surmount before these issues can be quantitatively studied in *Coenonympha* and, especially, before they can be used to truly test assumptions underlying species-level taxonomic decisions.

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Inter-island variation in the butterfly *Hipparchia* (*Pseudotergumia*) *wyssii* (Christ, 1889) (Lepidoptera, Satyrinae) in the Canary Islands

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Summary

Samples of the endemic Canary grayling butterfly, *Hipparchia* (*Pseudotergumia*) *wyssii* (Christ, 1889), were obtained from all five of the Canary Islands where it occurs. Each island population comprises a distinct subspecies but the differences between them are quantitative rather than qualitative ; hence a system is devised by which elements of the wing pattern are scored to permit quantitative analysis. The results demonstrate significant inter-island differences in wing size and wing pattern. The underside of the hindwing shows the greatest degree of inter-island variation. This is the only wing surface that is always visible in a resting butterfly ; its coloration is highly cryptic and it is suggested that the pattern was evolved in response to selection by predators long before *H. wyssii* or its ancestors reached the Canaries. Subsequent evolution of the details of the wing pattern differed from island to island because each island population was probably founded by few individuals with only a fraction of the genetic diversity of the species. It is postulated that the basic "grayling" wing pattern is determined by natural selection, but the precise expression of this pattern on each island is circumscribed by the limited gene pool of the original founders.

Résumé

Des exemplaires du Satyride *Hipparchia* (*Pseudotergumia*) *wyssii* (Christ, 1889), endémique des Iles Canaries, ont été récoltés dans les cinq îles de cet archipel où ils existent. Les populations de chaque île forment une sous-espèce distincte, mais les différences entre celles-ci sont plutôt quantitatives que qualitatives. On a donc établi un système basé sur certains éléments précis des ailes permettant une analyse quantitative. Les résultats ainsi obtenus prouvent l'existence de différences significatives entre les populations de chaque

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île en ce qui concerne la taille et le dessin des ailes. Le dessous des ailes postérieures est l'élément qui présente le plus fort degré de variation d'une île à l'autre. C'est en fait la seule partie de la surface des ailes qui est visible lorsque le papillon se pose. Son homochromie extrême est un élément de camouflage par mimétisme. On peut envisager que ce dessin a évolué du fait de la sélection par les prédateurs longtemps avant que *H. wyssii* ou ses ancêtres aient atteint les Canaries. L'évolution ultérieure des détails dans ce dessin des ailes fut différente d'une île à l'autre parce que la population de chaque île avait probablement été fondée par un petit nombre d'individus qui n'étaient chacun porteurs que d'une fraction de la diversité génétique de l'espèce. On peut donc penser que si le dessin typique «*Hipparchia*» du dessous des ailes postérieures est déterminé par sélection naturelle, la réalisation concrète de ce dessin sur chaque île se trouve différenciée du fait du stock de gènes incomplet des premiers arrivés «fondateurs».

Zusammenfassung

Der Augenfalter *Hipparchia* (*Pseudotergumia*) *wyssii* (Christ, 1889) ist auf den Kanaren endemisch. Untersuchungen an Material von allen fünf Inseln des Archipels, auf denen die Art vorkommt, ergaben, daß jede Inselpopulation eine eigenständige Unterart darstellt, die sich aber eher quantitativ als qualitativ von den anderen unterscheidet. Daher wurde ein System entwickelt, das durch die Untersuchung von Flügel-Zeichnungselementen eine quantitative Analyse erlaubt. Die Ergebnisse zeigen signifikante Unterschiede in Flügelgröße und Flügelzeichnung zwischen den Inselpopulationen. Die größte Variabilität weist die Unterseite des Hinterflügels auf. Dies ist die einzige Flügelfläche, die an einem ruhenden Falter stets sichtbar ist. Sie zeigt eine ausgeprägte Tarnfarbe, deren Muster vermutlich durch Feinddruck selektiert worden ist, bevor *H. wyssii* oder ihre Vorfahren die Kanaren erreichten. Die spätere Entwicklung der Details der Flügelzeichnung variiert von Insel zu Insel, weil jede Inselpopulation wahrscheinlich nur von wenigen Individuen -mit nur einen Bruchteil der genetischen Vielfalt der Art -begründet wurde. Es wird postuliert, daß das grundlegende *Hipparchia*-Flügelmuster durch natürliche Selektion bestimmt wird, aber die genaue Ausprägung dieses Musters auf jeder Insel vom begrenzten Genpool der ursprünglichen Gründer abhängt.

Introduction

The Canary grayling butterfly, *Hipparchia (Pseudotergumia) wyssii* (Christ, 1889) (Lepidoptera, Satyrinae) is endemic to the five Canary Islands of Tenerife, La Gomera, Gran Canaria, La Palma and El Hierro (Fig. 1). Until recently little was known of this species and even its presence on one island, La Palma, was in doubt (Leestmans, 1975) ; however a comprehensive review which followed several collecting trips (Wiemers, 1991) has established that the butterfly is relatively common

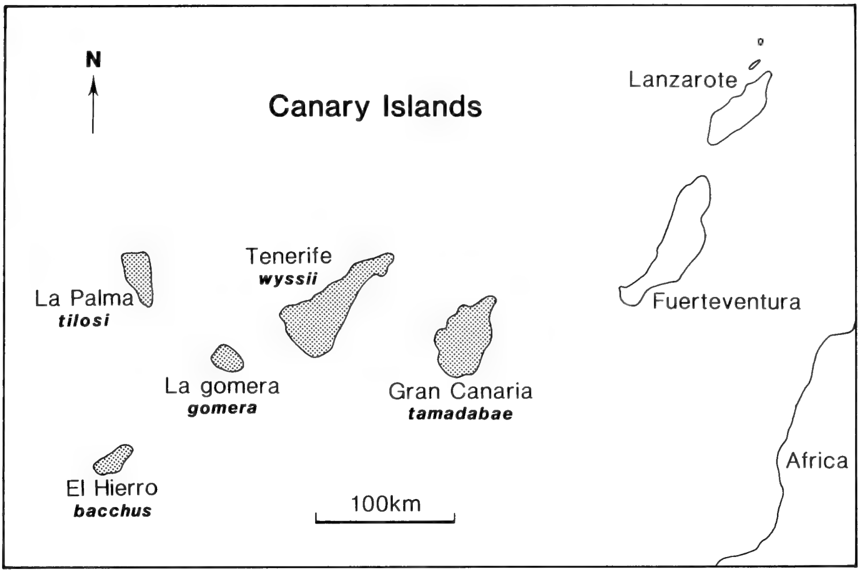

Fig. 1. The Canary Islands showing the distribution of the five subspecies of *Hipparchia wyssii.*

on Tenerife, La Gomera, La Palma and El Hierro (Herr Wiemers did not collect on Gran Canaria), and absent from the two eastern islands of Fuerteventura and Lanzarote, both of which are too dry for grass-feeding satyrine butterflies. This paper presents the results of our own sampling and field work on all five islands over the period 1987-91.

Grayling butterflies have a complex wing pattern, particularly on the underside, and the variation is difficult to quantify. Here we identify scorable and quantifiable phenotypic variation in wing pattern and coloration and use this to estimate the extent to which each island population is differentiated. Our paper is complementary to two previous analyses of variation in Canary Island satyrine butterflies : *Maniola jurtina* (Linnaeus, 1758) (Owen & Smith, 1990) and *Pararge xiphioides* Staudinger, 1871 (Owen & Smith, 1993).

The island populations

Each island population is distinctive and we treat each as a subspecies ; in contrast Wiemers (1991) recognizes four species : *H. wyssii* (Tenerife and Gran Canaria), *H. gomera* (La Gomera), *H. bacchus* (El Hierro) and *H. tilosi* (La Palma). We recognize five subspecies, one on each island while agreeing that some or all of them may have diverged sufficiently to be designated as species ; as we discuss later, there is rarely conclusive evidence either way (from crossing) when dealing with allopatric populations and, in its absence, splitting should be avoided (Corbet & Pendlebury, 1992). Plates 1 and 2 show the complex but distinctive underside patterns of males and females of each of the five subspecies.

H. wyssii wyssii (Christ, 1890). Tenerife. Mostly confined to *Pinus canariensis* forest at altitudes of 1300 — 1700 m and also found above the pine forest zone to 2300 m at Las Cañadas.

H. wyssii gomera (Higgins, 1967). La Gomera. Widespread in open country and light woodland at 300 — 1200 m. (There is no natural pine forest on La Gomera.)

H. wyssii tamadabae Owen & Smith, 1992. Gran Canaria. Mainly in *P. canariensis* forest at 300 — 500 m but extending to 1800 m and especially associated with shallow barrancos. Known chiefly from the north-west of the island.

H. wyssii bacchus (Higgins, 1967). El Hierro. Strongly associated with vineyards in barrancos at 300 — 700 m and extending in small numbers to 1500 m in laurel forest, but apparently rare or absent in *P. canariensis* forest.

H. wyssii tilosi Manil, 1984. La Palma. Apparently widespread in deep and steep-sided barrancos above 500 m in mixed laurel/pine forest on the east and north-east side of the island, but probably absent from the extensive *P. canariensis* forest around the Caldera de Taburiente. This subspecies may be much more split up into relatively isolated populations than the others.

On all islands the butterflies are on the wing in July and August but can occur as early as May and as late as September. The early stages from four islands are described in Wiemers (1991). The larvae are grass-feeders but precisely which species of grass are utilized in the wild has not been determined. There is one breeding generation a year. Adult butterflies occasionally visit flowers but are more often seen visiting damp patches and ripe fruit, especially grapes ; on Gran Canaria, and probably also on Tenerife, they probe cracks in the bark for pine resin. On Tenerife and Gran Canaria in particular there is a marked downhill movement in the evening and an uphill movement in the morning. Most individuals involved are females. This behaviour is spectacular, especially in places where movement is funnelled by a dry barranco ; we have no explanation for it but suggest it may be associated with locating egg-laying sites or with diurnal temperature changes.

The cryptic coloration of the underside, especially of the hindwing, is superb. When at rest on a pine trunk with the forewing lowered, a butterfly is almost impossible to see. When a resting butterfly is approached it raises its forewings and exposes the eyespots and at first walks around the tree trunk, sometimes circling the trunk several times. This is presumed to be anti-predator behaviour but we have no observations of successful predation, only an attempted catch by a blue tit, *Parus caeruleus* Linnaeus, 1758, and two unsuccessful strikes by a large asiliid fly. Some of the butterflies in our samples have wing damage suggestive of unsuccessful attacks by lizards.

The existence of *H. wyssii* on four of the Canary Islands has been known since 1888-9 (review in WIEMERS, 1991) but until 1966 it was well-known only from Tenerife, where it has been taken repeatedly. The rediscovery of populations on La Gomera and El Hierro in 1966 by Guichard and Ward (GUICHARD, 1967) was considered "unexpected and exciting...No butterflies of such distinctive appearance have been discovered in the Western Palaearctic Region for very many years" (HIGGINS, 1967). (Higgins was apparently unaware of earlier records for both islands dating from 1889 (REBEL & ROGENHOFER, 1894) and of NORDMAN (1935) for La Gomera.) The La Palma population remained unknown until 1983 (MANIL, 1984), possibly because its habitat is so inaccessible, while the true habitat and status of the Gran Canaria population seems to have been unknown until we discovered it in 1990 (OWEN & SMITH, 1992 and this paper).

Source of samples and methods of scoring

In 1987-91 we visited all the islands where *H. wyssii* occurs and collected random samples, from single locations in the case of four islands and from six different and isolated populations, four of which are new records for the species, on La Palma. Samples were deliberately limited because of uncertainty as to exactly how common the species is on each island ; in the event we discovered that no island population is endangered except by habitat destruction resulting from increased cultivation. The butterflies were pinned and set for more detailed examination. Sample sizes for each island are given in Table 1.

Fig. 2 is a diagram of grayling wings showing the numbering system for space(s) where spots (border ocelli) may be present or absent ; it

Table 1

Inter-island variation for forewing length (mm) in *H. wyssii* in the Canary Islands

Islands	T	G	C	P	H
	Males				
$\bar{x}$	29.2	29.5	28.0	29.7	30.1
s	1.7	1.0	1.0	1.6	0.5
n	3	16	24	25	6
	Females				
$\bar{x}$	29.7	31.7	28.8	29.5*	31.8
s	1.8	1.5	1.4	3.0	1.0
n	16	3	16	9	15

Island abbreviations : T = Tenerife, G = La Gomera, C = Gran Canaria, P = La Palma, H = El Hierro.

* One very small and otherwise aberrant female (22.8 mm), much the smallest individual of either sex recorded, substantially reduces the mean of this sample, without which it is 30.3 mm ($n = 8$).

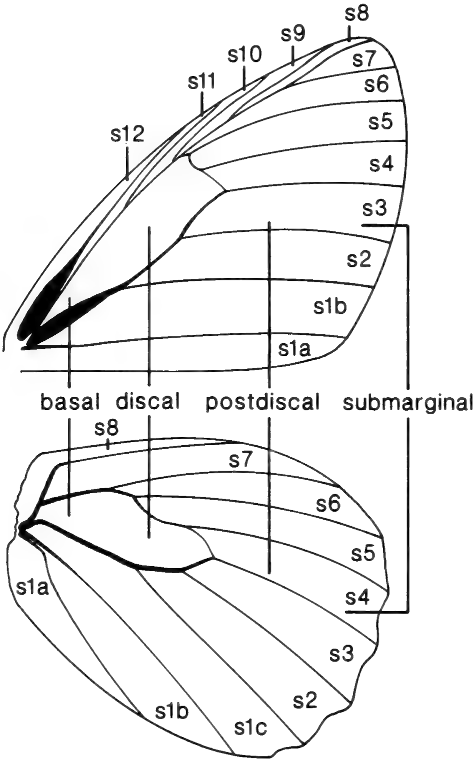

Fig. 2. Diagram of the wings of *Hipparchia wyssii* showing the nomenclature of spaces (s) and the location of other wing pattern elements mentioned in the text.

also shows the position of other elements of wing structure mentioned in the text. Each butterfly was examined by eye using a × 2 lens. All the scoring was done by one of us (DASS) to ensure consistency. The characters scored are listed in Appendix I. Forewing length was measured (with vernier calipers to an accuracy of 0.1 mm) from the apex to the point where the basal area joins the thorax. It was possible to measure forewing length in every specimen collected but for some other characters not all specimens could be scored because of damage.

Analysis

Size

Table 1 shows the mean forewing lengths for males and females. The rank order of forewing length for males is El Hierro > La Palma > La Gomera > Tenerife > Gran Canaria. If the single aberrant female from La Palma is omitted (Table 1), the rank order of forewing length for females is similar : El Hierro > La Gomera > La Palma > Tenerife > Gran Canaria.

Table 2 shows the results of a one-way ANOVA for forewing length. The overall values of variance ratios (*F*) are significant for both males and females at the 0.1 per cent level, indicating that forewing length (which reflects body size) has diverged significantly among the island populations. Individual island comparisons are shown in Table 2 only where they are significant. Of the seven significant comparisons, five

Table 2

One-way analysis of variance for forewing length in *H. wyssii* from the Canary Islands

Source of variation	Degrees of freedom	Variance ratio (*F*)	Probability
	Males		
All islands	4,69	7.25	<0.001
C v G	1,72	12.51	<0.001
C v P	1,72	22.13	<0.001
C v H	1,72	13.67	<0.001
	Females		
All islands	4,54	6.88	<0.001
T v H	1,57	11.39	<0.01
C v G	1,57	6.95	<0.05
C v H	1,57	22.79	<0.001
P v H	1,57	9.88	<0.01

Island abbreviations as in Table 1. Comparisons for individual island pairs are included only if statistically significant.

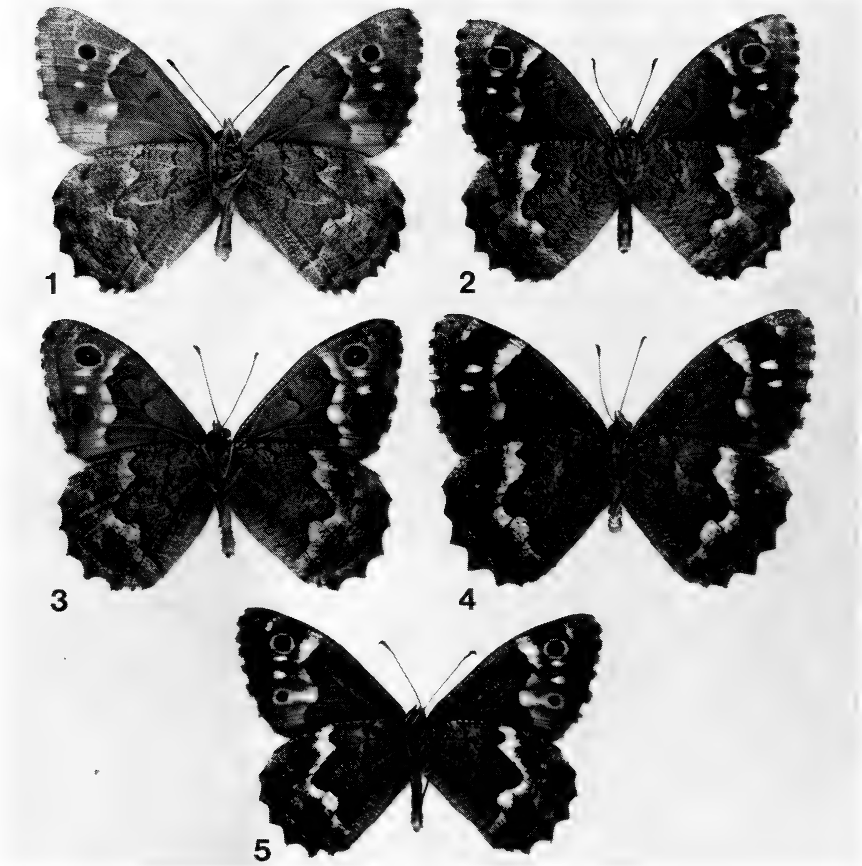

Plate 1. *Hipparchia wyssii*, undersides of males (actual size).
1 — *H. w. wyssii* (Tenerife) ; 2 — *H. w. gomera* (La Gomera) ; 3 — *H. w. tamadabae* (Gran Canaria) ; 4 — *H. w. bacchus* (El Hierro) ; 5 — *H. w. tilosi* (La Palma).

involve Gran Canaria (the smallest subspecies) and four El Hierro (the largest). Therefore, size may be a diagnostic character for at least these two islands but it is possible that larger samples would reveal that all five populations are statistically different in size. The marked difference in size between Gran Canaria and El Hierro butterflies can be seen in Plates 1 and 2.

Hindwing border ocellus (spotting) phenotypes

A list of hindwing spotting phenotypes is given in Appendix III. The spots, which belong to the border ocellus system (Nijhout, 1991), are

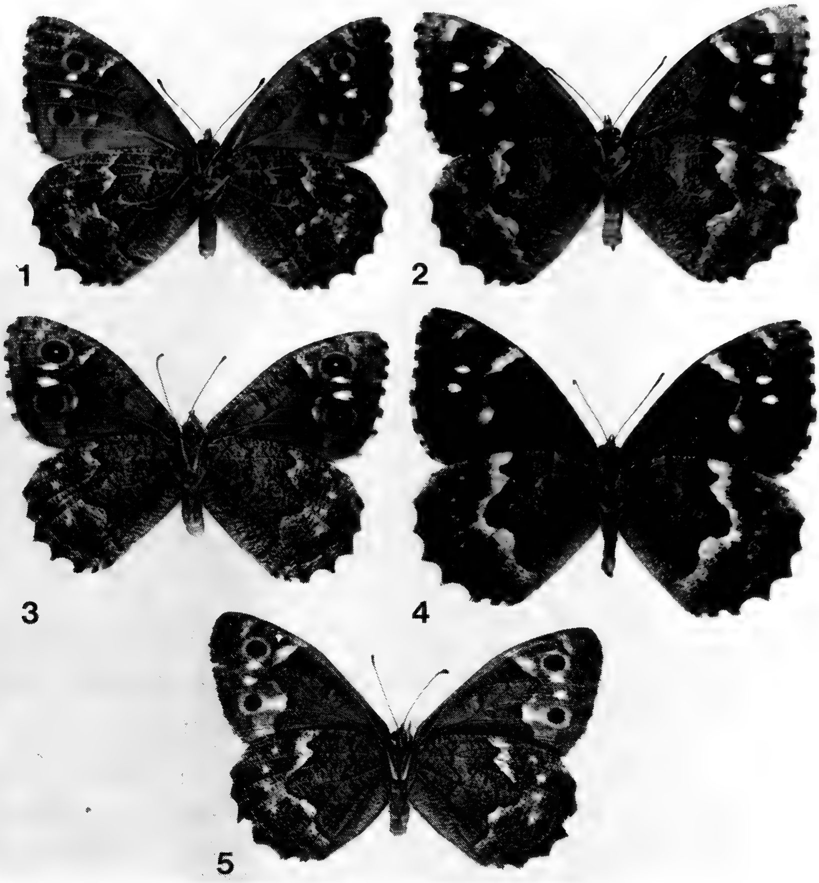

Plate 2. *Hipparchia wyssii*, undersides of females (actual size).
1 — *H. w. wyssii* (Tenerife) ; 2 — *H. w. gomera* (La Gomera) ; 3 — *H. w. tamadabae* (Gran Canaria) ; 4 — *H. w. bacchus* (El Hierro) ; 5 — *H. w. tilosi* (La Palma).

numbered antero-posterially from the costal side as follows : 1 (space 6), 2 (s5), 3 (s4), 4 (s3), 5 (s2) (the position of the spaces is shown in Fig. 2). Spots 1 — 4 are pale ochreous or white on the upperside but invariably white on the underside. Spot 5 is always black and may be white-pupilled (underlined) or ringed with a yellowish halo (superscript bar).

Table 3 shows the distribution of hindwing spotting phenotypes on each of the five islands. As shown, we recorded 18 upperside (UPH) phenotypes (A-R), and 22 underside hindwing (UNH) phenotypes (1-22).

Table 3

Distribution of the hindwing upper and underside border ocellus phenotypes
of *H. wyssii* (see Appendix III for codes) on the five Canary Islands where it occurs

Phenotype	T	G	C	H	P	Phenotype	T	G	C	H	P	Phenotype	T	G	C	H	P
§ A01			+			# B17	+			+		§ H15					+
§ A02			+			# B18	+			+		§ H17					+
§ A07			+			* B19	+					§ H20					+
# A09	+		+			# B20	+	+	+	+		* I21			+		
§ A12		+				# B21			+			* J20					+
§ A13		+				* B22	+					* K07				+	
§ A17			+			* C20	+					* K20				+	
# B01	+	+	+	+		§ C21					+	* L07					+
§ B02			+			* D18	+					* L20	+				
# B03	+	+		+	+	§ E09					+	# L21			+		+
§ B04			+			* E15	+					* M20					+
# B05	+		+			* E17					+	* N02			+		
* B06	+					§ E20					+	* O20					+
# B07		+	+	+		§ E21					+	* P08			+		
# B08		+	+			* F07				+		* P16			+		
§ B09					+	* F14			+			* P20					+
§ B10				+		* F15				+		* P21	+		+		
* B11	+					§ F20					+	* Q20					+
§ B15		+			+	* G20					+	* R21			+		
* B16			+														
												Total phenotypes	16	8	22	11	20

§ recorded in males only (19), * recorded in females only (28), # recorded in both sexes (11). Island abbreviations as in Table 1.

58 different combinations were recorded ; the theoretical maximum is 396 though the actual number is probably far less. Considering the small size of some samples, however, many more phenotypes would be expected in larger samples, especially in males from Tenerife (n = 3) and females from La Gomera (n = 3). Nineteen phenotypes occur in males only, 28 in females only and 11 in both sexes : females are thus more variable than males.

Table 4 summarizes inter-island differences in the distribution of hindwing phenotypes and compares hindwing diversity on each of the five islands. Of the 58 hindwing phenotypes recorded only 12 (≃ 20%) occur on more than one island, none is found on all five islands and only three (≃ 5%) occur on four islands. This alone suggests considerable inter-island diversification.

The distance coefficients for phenotypes shared with other islands (Table 6D) show that La Palma has the most distinct population, followed by Gran Canaria, Tenerife and La Gomera/El Hierro. La

Table 4

Analysis of the inter-island distributions (Table 3)
of the hindwing phenotypes of *H. wyssii* (Appendix III) in the Canary Islands,
with the phenotypic diversity on each island

Islands	T	G	C	H	P	*N*
Number of phenotypes (both sexes)	16	8	22	11	20	58
Sample size	18	18	36	21	30	123
Number phenotypes shared between 4 islands	3	3	2	3	1	3
Number phenotypes shared between 3 islands	0	1	1	1	0	1
Number phenotypes shared between 2 islands	5	2	5	2	2	8
Total shared phenotypes	8	6	8	6	3	12
Mean % phenotypes shared with other islands	15.0	16.4	11.0	16.3	4.1	—
Mean phenetic distance from other islands	0.42	0.42	0.47	0.45	0.52	
Total unique phenotypes	8	2	14	5	17	46
Per cent unique phenotypes	50.0	25.0	63.6	45.5	85.0	—
Margalef Diversity Index (D_{Mg})	5.19	2.42	5.86	3.29	5.59	
Berger-Parker Diversity Index ($1/d$)	4.50	2.25	5.14	4.20	7.50	—

Island abbreviations as in Table 1.

Palma is also the most distinctive population in terms of the percentage of unique phenotypes, followed again by Gran Canaria and Tenerife.

Small sample size in one or the other sex from some islands necessitates combining sexes to estimate phenotypic diversity. Although this procedure inevitably involves the loss of some resolving power, the results are nevertheless unambiguous. We use two contrasting measures of diversity, the Margalef Index and the Berger-Parker Index (Magguran, 1988). The former is primarily a measure of richness (number of phenotypes) (Clifford & Stephenson, 1975) and has the disadvantage that it is strongly influenced by sample size (Southwood, 1978) ; the latter emphasises evenness (or dominance) and is little affected by sample size (May, 1975). In this case, where all samples are fairly small, the Berger-Parker Index is preferred although encouragingly the rankings for the two indices are in substantial agreement. The La Palma (Berger-Parker) and Gran Canaria (Margalef) populations have the highest diversity, El Hierro and La Gomera (especially) the lowest, with Tenerife intermediate (both indices agree on the ranking of the latter three islands).

In general the larger islands (Tenerife, Gran Canaria and La Palma) are more diverse than the smaller (El Hierro and La Gomera), as could be predicted from biogeographical theory (MacArthur & Wilson, 1967). The high diversity on La Palma, in particular, is enigmatic : it may result from independent evolution of sub-populations in relative isolation within deep barrancos, a situation which probably does not prevail on the other islands.

Table 5
Mean values for spots, pupils and halos comprising the hindwing border ocellus system in *H. wyssii* from the Canary Islands

Islands	T	G	C	H	P
			Males		
UPH spot average (max. 5)	1.0	0.9	0.7	1.0	1.7 §
UNH spot average (max. 5)	3.5	2.8	2.7	1.8	4.3 §
Pupil average (max. 6)	0.0	0.1	2.0 §	0.0	0.2
Halo average (max. 6)	1.7	1.7	0.5	1.0	2.2 §
N (N)*	3 (2)	16	24 (21)	6	25 (22)
			Females		
UPH spot average (max. 5)	1.6	1.0	2.7	1.8	3.8 §
UNH spot average (max. 5)	3.9	2.5	3.9	3.3	4.8 §
Pupil average (max. 6)	0.5	0.0	3.1 §	0.0	0.1
Halo average (max. 6)	2.4	2.0	2.3	1.2	4.7 §
N (N)*	16	3 (2)	16 (15)	15	9 (8)

* Numbers in parenthesis are sample sizes for spot averages reduced due to hindwing damage in some specimens. § Sample means significantly different (in *t* tests) from others in the same row. Island abbreviations as in Table 1.

Table 5 shows the UPH and UNH spot averages for males and females for each island. Correlation for UPH and UNH spot number in individuals is low and not significant in either males ($r = 0.070$, $n = 68$) or females ($r = 0.073$, $n = 55$) ; Nijhout (1991) has emphasised that dorsal and ventral wing coloration patterns develop from epithelial monolayers within separate compartments and that correlation between them is by no means inevitable. As shown, La Palma has the highest values for spot average for both UPH and UNH. El Hierro and La Gomera have the lowest values with Tenerife and Gran Canaria intermediate.

The frequency of white pupils in the six black spots (border ocelli) (UPF/UNF s6 and s3 and UPH/UNH s2) and of the yellow halos around the same spots, provides a set of characters additional to hindwing spotting which can be used to differentiate populations. Table 5 gives pupil and halo averages for males and females for each island. The sum of pupils (maximum 6) and halos (maximum 6) for an individual butterfly gives a measure which we call spot enhancement (maximum 12) ; both pupils and halos render the black spots more distinctive and conspicuous. Males and females from La Palma and Gran Canaria have significantly higher enhancement values than the other populations but it is obtained by different means : mainly by pupillation on Gran Canaria (a consistently diagnostic feature of ssp. *tamadabae*) and by the development of halos in ssp. *tilosi* from La Palma. Both features are recorded from some of the other islands but less distinctly and much less frequently. On La Palma and Gran Canaria, the black spots tend to be larger and, when combined with white pupils and yellow halos, they are rendered much more apparent.

The ssp. *bacchus* phenotype is also highly distinctive in a quite different way from ssp. *tilosi* or ssp. *tamadabae*, because of the intense contrast between the postdiscal black line (element **f** of the central symmetry system (Nijhout, 1991)) and the band of white background immediately distal to it, especially on the UNH (Plates 1 and 2) ; ssp. *bacchus* has low values for spot average and much the lowest development of spot enhancement (Table 5). As the background of the *bacchus* wing is extensively melanised, several other black pattern elements (**d**, **e** and **i** (Nijhout, 1991)) are also relatively obscured. Subspecies *gomera* is intermediate between ssp. *bacchus* and ssp. *wyssii* in all the above respects (Plates 1-2).

Table 6
Matrices showing mean Euclidean distances (*MED*)
for five *H. wyssii* OTUs in the Canary Islands :
(A) males, (B) females, (C) combined sexes,
(D) hindwing spotting phenotypes (both sexes) (Table 3, Appendix III).
A-C are based on 34 non-metric characters and D
on numbers of phenotypes shared between islands (Table 4)

		T	G	C	H	P	
	T	—	0.359	0.409	0.371	0.544	
	G	0.410	—	0.522	0.321	0.585	
A	C	0.296	0.434	—	0.519	0.580	B
	H	0.484	0.330	0.469	—	0.588	
	P	0.483	0.399	0.507	0.509	—	
	T	—	0.842	0.839	0.750	0.970	
	G	0.386	—	0.846	0.733	0.923	
C	C	0.355	0.479	—	0.900	0.976	D
	H	0.433	0.326	0.494	—	0.967	
	P	0.513	0.497	0.544	0.548	—	

Kendall's rank correlation for A and B is not significant ($\tau = 0.4$, $P = 0.11$) ; C and D are significantly correlated ($\tau = 0.822$, $P = 0.04$). Island abbreviations as in Table 1.

Phenetic distance coefficients

The phenotypes of all members of the genus *Hipparchia* Fabricius, 1807 are difficult to measure as much of the variation is quantitative and therefore judgment of it subjective. Hence for the calculation of phenetic distance coefficients (Table 6), we have chosen 34 non-metric characters (Appendix I) which are discrete (i.e. can be consistently scored as present or absent) and variable in frequency within or between islands. This statement does not imply that these characters are the only ones by which the five island populations can be compared and differentiated, nor that they are necessarily even the most distinctive. Many characters are manifested only or mainly in males (9) or females (7) ; those which are variable in both sexes (18) nevertheless differ in frequency and so they are scored separately for males and females. Therefore the matrices (Table 6) are based on 27 characters for males, 25 for females and 52 for the combined sexes. As shown in the character matrix (Appendix II), few characters are absolutely diagnostic, most differing only quantitatively between islands. Hence each character score is weighted (0-100%) for its comparative frequency. The data in Table 6 represent the Euclidean distance *MED* (Sneath & Sokal, 1973) between pairs of island populations (OTUs). *ED* is calculated for each OTU (subspecies) pair using the formula :

$$ED_{jk} = [\Sigma(X_{ij} - X_{ik})^2]^{1/2}$$

where X_{ij} and X_{ik} are the scores of OTUs (subspecies) j and k for character i. Mean Euclidean distances (*MED*) over all characters are calculated as :

$$MED_{jk} = \sqrt{[\Sigma(X_{ij} - X_{ik})^2]/n}$$

where n is the number of characters.

Comparing the distance values (*MED*) between sexes (Table 6A, B, Fig. 3A, B) it is clear that females have in general diverged further than males. In the case of La Palma this applies to the female *MED* values compared to all other islands ; for Gran Canaria it is confined mainly to the comparison with Tenerife. Furthermore, the differences between the male and female phenograms (Fig. 3), and the absence of any significant rank correlation between their inter-island phenetic distances (Table 6), strongly suggest that there has been a degree of independence in the evolution of the phenotype of the two sexes, the male being the more conservative .

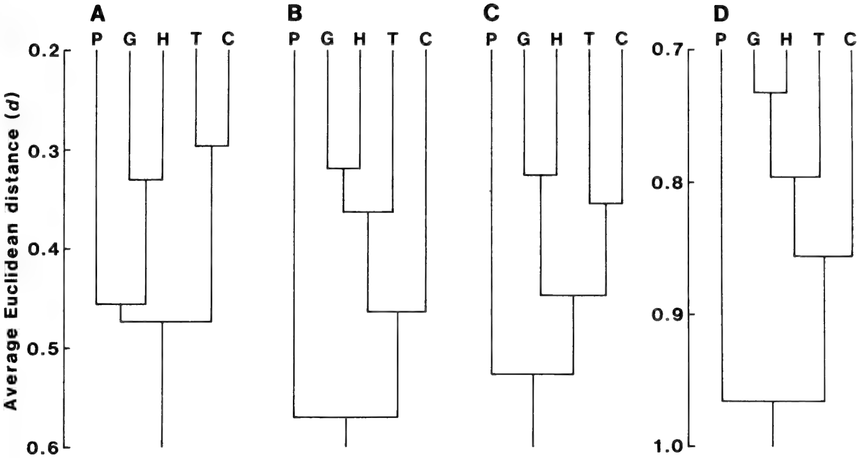

Fig. 3. Phenograms, derived by UPGMA, showing the mean Euclidean distances (*MED*) (Table 6) between the five subspecies of *Hipparchia wyssii*: A, males; B, females; C, combined sexes; D, hindwing border ocellus phenotypes (both sexes) shared between islands (Table 3). Island abbreviations as in Table 1.

Considering combined sexes (Table 6C), La Palma (mean distance = 0.523) is the most distinctive followed by Gran Canaria (0.468). El Hierro (0.450) is intermediate, with Tenerife and La Gomera (both 0.422) the least distinctive on average. The two most similar populations are El Hierro and La Gomera. However, there is no rank correlation (Siegel & Castellan, 1988) between the geographical distances separating islands and phenetic distances (Kendall's τ (tau) = 0.422; $P = 0.11$).

In Table 6D we compare the islands by numbers of shared hindwing phenotypes. The isolation of La Palma and the closeness of La Gomera and El Hierro are again clear and, as above, there is no rank correlation between the physical distance separating islands and the number of shared phenotypes ($\tau = 0.244$; $P = 0.38$). Encouragingly, however, the two methods of inter-island comparison (Table 6C, D) are themselves significantly correlated by rank ($\tau = 0.822$; $P = 0.04$).

Interpretation of inter-island variation

The phenograms in Fig. 3 are derived by the UPGMA method (Sneath & Sokal, 1973) from the data in Table 6. The relative isolation of the La Palma subspecies is evident in all the phenograms ; La Gomera and El Hierro form a cluster ; Tenerife and Gran Canaria may also form a cluster, possibly for male phenotypes only (Table 6A, 6C), but 6B and 6D suggest that Tenerife is closer to La Gomera/El Hierro with Gran Canaria more isolated. The raw data for males (Table 6A) indicate that ssp. *tilosi* (La Palma) is closer to ssp. *gomera* (La Gomera) than to any other but this is not the case for females. The phenetic distance of *ssp. tilosi* females from all other subspecies would suggest either a comparatively early dichotomy from the ancestral stock or more recent but rapid evolution. To explain this anomaly it is necessary to postulate different rates of evolution in males and females, the former being relatively conservative and the latter evolving rather rapidly, especially on La Palma. All data sets (Table 6) show that *ssp. tamadabae* (Gran Canaria) is closest to *ssp. wyssii* (Tenerife). In this case too, however, there is a sex difference, the males being much closer than the females. The El Hierro subspecies (ssp. *bacchus*) is undoubtedly closest to ssp. *gomera* and is equally distinctive, mainly due to the dark background (unscored) (Plates 1 & 2), in both sexes. It should be noted, however, that WIEMERS (1991) observed that the eggs of these two subspecies are quite dissimilar.

The origin and relationships of *H. wyssii*

There are three other species belonging to the subgenus *Pseudotergumia* Agenjo, 1947 (KUDRNA, 1977). If examined comparatively in the manner advocated by HARVEY & PAGEL (1991), they are the outgroup for reconstructing ancestral character states. *H. fidia* (Linnaeus, 1767) is a west Mediterranean species ranging from Morocco, Algeria and Tunisia through Portugal, Spain and S. France to Italy ; *H. pisidice* Klug, 1832 occurs in the Middle East from Sinai through Jordan, Palestine, Lebanon and Syria to south Turkey ; *H. tewfiki* (Wiltshire, 1949) is a relict endemic restricted to Yemen and southwest Arabia. All three species share with *H. wyssii tamadabae* the white pupilling of the two forewing ocelli in s6 and s3 (UPF and UNF). These characters are likely to be primitive for the subgenus and their absence from most individuals of the other subspecies of *H. wyssii* is probably due to loss. There are several other similarities between ssp. *tamadabae* and the other *Pseudotergumia* species (the nomenclature of the following pattern elements follows NIJHOUT (1991) : first, the bold black proximal band of the central symmetry system (element **d**), which bisects the discal cell (UNF) ; second, bold discal spots (element **e**) on the discoidal vein (UNF) and, third, bold proximal (medial) and distal (postmedial) bands (elements **d** and **f**) of the central symmetry system (UNH), given in our original description of ssp. *tamadabae* (Owen & Smith, 1992). All things considered, it seems likely that *H. wyssii tamadabae* is closest to the ancestral *Pseudotergumia* (and *Hipparchia*) phenotype. In other words, the states of some of the above characters in most individuals of *H. wyssii* ssp. *wyssii, gomera, bacchus* and *tilosi* are derived.

The origin of *H. wyssii* itself is a matter for conjecture. On the evidence of present distributions, an origin for *H. wyssii* from *H. fidia* stock, which inhabited the western Mediterranean area, seems the most plausible. Indeed, while admitting that *Hipparchia* phenotypes are in general conservative, the adult phenotype of *H. fidia* is in many respects close to *H. wyssii tamadabae*. However, from a comparison of the male genitalia and androconia, Kudrna (1977) believed *H. wyssii* to be closer to *H. tewfiki* than to either *H. fidia* or *H. pisidice*. Judging from his excellent figures of the very similar genitalia and androconia of all the *Pseudotergumia* species, his conclusion requires exceedingly fine distinctions to be made, mainly on grounds of size. As is commonly the case when genitalia characters are used in insect taxonomy, no allowance was made for allometry (Gould, 1966) : *H. tewfiki* is considerably smaller than all other species of *Pseudotergumia* but, of the subspecies of *H. wyssii* examined by Kudrna, is closest in body size to ssp. *wyssii* (which he believed inhabited both Tenerife and Gran Canaria). The above remarks notwithstanding, as the only worker to have examined all known museum specimens of the four *Pseudotergumia* species, we tentatively accept Kudrna's conclusion that *H. wyssii* is closer to *H. tewfiki* than to *H. fidia*. In view of the conservatism of *Hipparchia* adult phenotypes and the considerable continuous variation between individuals within taxa, a protein or DNA study is needed to reach more robust conclusions.

If *H. wyssii* and *H. tewfiki* are indeed closely related then their present distributions, in the Canaries and southwest Arabia, respectively, are highly disjunct. To account for the presence of *H. wyssii* in the Canary Islands, it is therefore necessary to invoke both vicariance and several island-hopping events. We argue that neither is improbable as both are prevalent features of the flora and fauna of the Canary Islands. First, during the Miocene, southern Europe and the present Sahara Desert area were covered with subtropical to tropical evergreen forests (Axelrod, 1986). As drier climates spread through the Upper Miocene and Pliocene, disjunctions in range developed, which are well-documented for the flora (Bramwell, 1976) resulting in highly disjunct distributions between, on the one hand, the Canary Islands and, on the other, far-distant locations such as Arabia, Socotra, Mauritius, the East African highlands, the Himalayas and south Asia. Two of these disjunctions are particularly relevant to a possible scenario for the origin of *H. wyssii* : *Pinus canariensis* may be most closely related to *P. roxburghii* of the western Himalaya, with fossil relatives in southwest Asia (AXELROD, 1986) ; the genus *Appollonias* (Lauraceae), one of the four lauraceous species found in the *laurisilva*, has only two living species, *A. barbajuna* in the Canaries and *A. arnotti* in south India (SUNDING, 1979). Moreover, there are parallel examples among butterflies : the distribution of *Vanessa indica* (Herbst, 1794) (Nymphalidae), with distinct subspecies in Macaronesia (the Canaries and Madeira) and south Asia, has attracted recent attention (LEESTMANS, 1978 ; SHAPIRO, 1992a, 1992b) ; the genus *Cyclyrius* Butler, 1897 (Lycaenidae), which has only two living species, *C. webbianus* (Brullé, 1840) in the Canaries and *C. mandersi* (Druce, 1907) from Mauritius, presents a similar case (OWEN & SMITH, 1993).

There is considerable evidence that many genera of butterflies from several families and subfamilies, including some satyrines (PORTER & GEIGER, 1988 ; PORTER & SHAPIRO, 1991), are slow-evolving or bradytelic (SIMPSON, 1944). We believe that *Hipparchia*, in particular the ancestor of *tewfiki-wyssii* is probably a bradytelic taxon and that *H. wyssii* has a relatively ancient origin (LARSEN, 1984) in the Miocene, say 10 — 15 Ma. The first dispersal event, presumably from North Africa, was probably to the eastern islands of Gran Canaria and Fuerteventura, possibly at the same time as the invasion of the *laurisilva* and *P. canariensis* forest and before these islands became arid. The second dispersal event may have been from Gran Canaria to La Gomera. However, the low phenotypic diversity on La Gomera, compared to Gran Canaria, and indeed all other islands, suggests a bottleneck effect at introduction which is still reflected in the modern population. Subsequent island hops would follow, first to Tenerife, not earlier than 6 Ma (SCHMINKE, 1976) and then to El Hierro and La Palma during the Pleistocene (2 — 0 Ma). The increasing aridity of the Sahara region during the Pliocene would then produce the vicariance event which split the *tewfiki-wyssii* ancestor into two relict species.

Comparative morphology and high phenotypic diversity, as well as the antiquity of Gran Canaria (SCHMINKE, 1976), support the proposed ancestral status of ssp. *tamadabae*. Whether ssp. *wyssii* on Tenerife originated from La Gomera or Gran Canaria (or both) remains an open question, each being almost equally likely on grounds of comparative morphology (Table 6). The data indicate that ssp. *bacchus* (El Hierro) originated from La Gomera, the nearest source, at a date which must have been ≤ 2 Ma ago.

The case of ssp. *tilosi*, however, appears anomalous and defies simple interpretation. While it is undoubtedly closest to ssp. *gomera* (Table 6), it is the most distinct of all five subspecies (Fig. 3) and shares the smallest number of hindwing phenotypes with other subspecies ; it also shows the highest phenotypic diversity (Table 4). We suggest above that the fragmented distribution of ssp. *tilosi* into many small isolated populations, a situation which does not apply to the other subspecies, may have resulted in numerous founder effects with unusual and differing starting sets of alleles ; sub-population differences might further intensify under subsequent genetic drift. Our collection is much too small to hope to find quantitative differences between the six sub-populations from La Palma represented, but the high phenotypic diversity in the bulked sample may reflect heterogeneity arising from the fragmented population structure of this subspecies.

However, the fact that ssp. *tilosi* is the most distant (phenetically) from all other subspecies and occurs on the island known to be the youngest (≤ 2 Ma) (SCHMINKE, 1976) and furthest from a continental source of recruitment, suggest two other possible interpretations of the evolutionary history of *H. wyssii*. First, the species may have colonised the Canary archipelago only within the last two million years, in which case the diversification we describe occurred within the Pleistocene or later. If this is the case, then rapid evolution has occurred on El Hierro and (especially) La Palma. It follows from this that the pre-Pleistocene geological history of the islands would be irrelevant to any attempt to reconstruct the evolution of *H. wyssii*. Alternatively, the species may have reached the eastern islands a long time ago but dispersed to La Palma and El Hierro, where it has undergone rapid evolution, comparatively recently. This last interpretation best fits the facts.

Discussion

Graylings are essentially "underside" butterflies. Only rarely is the upperside visible and it is the underside that has the intricate and characteristic patterning. When a butterfly comes to rest, the underside of the forewing is well-exposed and its spots are conspicuous. After a short interval, the forewing is lowered and hidden by the hindwing, and the butterfly is beautifully camouflaged against the background of rock or tree trunk. If alerted, it raises the forewing and the eyespots are again visible. This behaviour is widespread among members of the Satyrinae but is particularly well-developed in *Hipparchia* and it is usually interpreted as anti-predator strategy. The forewing eyespots catch the attention of a predator which may then strike at a non-vulnerable part of the wing (Brakefield, 1984), enabling the butterfly to escape by flying away. If there is no strike, the butterfly assumes the resting position with the forewing concealed. Our observations on all subspecies of *H. wyssii* suggest that this presumed anti-predator behaviour is the norm. The rarely exposed upperside is rather uniformly dark and may function in thermoregulation, though only in flight, as *Hipparchia* group species are exclusively lateral baskers at rest (Shreeve & Dennis, 1992) : it is probably never involved in anti-predator behaviour.

Hence, we view the ground plan of the underside pattern of all five subspecies as having evolved in response to selection by predators ; most of this evolution must have occurred before what is now *H. wyssii* reached the Canary Islands. Assuming a mainland origin for *H. wyssii*, the initial colonisation of any one of the islands may have involved few individuals ; indeed a single fertilised female is all that is required. Subsequent colonisation of other islands might similarly involve few individuals. Each colonisation has produced relatively large but isolated populations which could easily have been founded with only a fraction of the genetic diversity of its source population(s) leading to selective and epigenetic constraint. The restricted gene pool of each founder population would thus be unique to each island and differ stochastically from all other islands : this alone could account for most of the inter-island differentiation we have described. Genetic drift in the initially small populations of founders would be expected to lead to a further loss of genetic diversity and to the fixation of inter-island differences, which are mainly so minor that their influence on survival may be trivial.

Nijhout (1991) emphasises that small changes in the source or steepness of diffusion gradients for theoretical morphogens, thresholds for the expression of alternative pigment genes and pattern elements and the timing of the sequence of morphogenetic events, can produce quite profound changes to the visible phenotype. We believe that developmental constraint, probably involving very few gene loci with alternative alleles, has produced the high proportion of unique character combinations that now occur on each island. The overall result is that the distinct grayling phenotype is retained but its precise expression on each island is different and dependent on the genetic history of each population. The hindwing underside is the most complex of a grayling's wing surfaces and it is this which is most often exposed to potential predators : it is a cryptic wing surface but the precise means by which crypsis is attained differs from island to island.

Of the 30 species of butterfly found on the Canary Islands, four (including *H. wyssii*) exhibit inter-island differentiation in wing pattern morphology, while others probably do so but have not been subjected to detailed analysis. In all four cases, the island differences are quantitative rather than qualitative. In two species, *Maniola jurtina* and *Pararge xiphioides*, subspecific names have not been given, while in the other two, *Gonepteryx cleopatra* (Linnaeus, 1767) and *H. wyssii*, subspecific (or specific) status is based on small differences in adult size, wing pattern and the structure of genitalia (Kudrna, 1975, 1977), and in the latter case, also on egg and larval morphology (Wiemers, 1991). While these features differ slightly between islands, they vary only to an extent, as in comparisons between Palaearctic and Nearctic *Aglais* Dalman, 1816 and *Nymphalis* Kluk, 1802, that either species or subspecies might be expected to differ (Miller & Miller, 1990). To demonstrate speciation more positively would require cross-breeding or better, analysis of mtDNA. However, our view is that, although it hardly matters whether the island populations of *H. wyssii* are designated as species or subspecies, we have found no compelling evidence for full speciation and are thus persuaded to leave them as well-differentiated subspecies.

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APPENDIX I

Characters used for analysis of inter-island differences in *Hipparchia wyssii* in the Canary Islands

UPF
1. Small ochreous border ocellus (**h**) in s7. #
2. Black border ocellus in s6 (**h**) with white pupil.
3. Black border ocellus in s6 (2) ringed with yellowish halo.
4. Pale submarginal spot (**h**) in s5. *
5. Pale spot in s5 (4) white (+) or brown. *
6. Pale submarginal spot (**h**) in s4. *
7. Pale spot in s4 (6) white (+) or brown. *
8. Black border ocellus (**h**) in s3. *
9. Black border ocellus (8) in s3 with white pupil. #
10. Black border ocellus (8) in s3 ringed with yellowish halo.
11. Pale postdiscal spot in s6. *
12. Above spot (11) in s6 white (+) or pale brown. #
13. Pale postdiscal spot in s3. *

UPH
14. Pale ochreous or white border ocellus (**h**) in s6 (spot 1).
15. Similar ocellus (**h**) in s5 (spot 2).
16. Similar ocellus (**h**) in s4 (spot 3). #
17. Similar ocellus (**h**) in s3 (spot 4).
18. Small submarginal black border ocellus (**h**) in s2 (spot 5). *
19. Spot 5 (18) with minute white pupil. #
20. Spot 5 (18) ringed with narrow yellowish halo. #

UNF
21. Large black border ocellus (**h**) in s6 with white pupil.
22. Spot in s5 fused with halo of border ocellus in space 6.
23. Black border ocellus (**h**) in s3 with white pupil. #
24. Black border ocellus (**h**) in s3 ringed with yellowish halo.
25. s3 between elements **f** (postmedial line) and **h** ochreous (+) or brown.
26. Postdiscal area of s2 ochreous (+) or brown.
27. Diffused ochreous spot proximal to element **d** in discal cell. *

UNH
28. Diffuse white submarginal border ocellus (**h**) in s6 (spot 1).
29. Similar spot (**h**) in s5 (spot 2).
30. Similar spot (**h**) in s4 (spot 3).
31. Similar spot (**h**) in s3 (spot 4).
32. Black spot in s2 with minute white pupil.
33. Pale patches immediately lateral to postmedial line (**f**) flecked white (+) or grey.
34. Above patches (33) fused to form irregular but uninterrupted stripe.

Letters in bold type identify the probable homologies of pattern elements according to the nymphalid ground plan (Nijhout, 1991). s = space (Fig. 2) UPF = upperside forewing ; UPH = upperside hindwing ; UNF = underside forewing ; UNH = underside hindwing ; + = present ; characters expressed or variable only in one sex are marked * for males (9) and # for females (7) ; all other characters (18) are scored in both sexes.

APPENDIX II

Character matrix for *H. wyssii* from the Canary Islands.
The data are expressed as percent occurrence

Character number	Males					Females				
	C	T	G	H	P	C	T	G	H	P
UPF 1	—	—	—	—	—	25.0	12.5	0.0	0.0	0.0
2	50.0	0.0	0.0	0.0	0.0	93.8	0.0	0.0	0.0	0.0
3	8.3	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	100.0
4	91.7	66.7	75.0	100.0	80.0	—	—	—	—	—
5	36.4	0.0	16.7	83.3	15.0	—	—	—	—	—
6	91.7	100.0	100.0	100.0	100.0	—	—	—	—	—
7	45.5	0.0	37.5	100.0	80.0	—	—	—	—	—
8	87.5	100.0	100.0	100.0	100.0	—	—	—	—	—
9	—	—	—	—	—	31.3	0.0	0.0	0.0	0.0
10	0.0	0.0	0.0	0.0	20.0	0.0	18.8	0.0	0.0	100.0
11	8.3	0.0	93.8	100.0	16.0	—	—	—	—	—
12	—	—	—	—	—	18.8	43.8	66.7	93.3	25.0
13	20.8	0.0	87.5	100.0	96.0	—	—	—	—	—
UPH 14	—	—	—	—	—	33.3	6.3	0.0	20.0	42.9
15	0.0	0.0	0.0	73.3	22.7	53.3	18.8	0.0	66.7	100.0
16	—	—	—	—	—	33.3	18.8	0.0	0.0	42.9
17	0.0	0.0	0.0	0.0	40.9	46.7	25.0	0.0	0.0	85.7
18	66.7	100.0	87.5	100.0	100.0	—	—	—	—	—
19	—	—	—	—	—	13.3	6.7	0.0	0.0	0.0
20	—	—	—	—	—	0.0	6.7	0.0	0.0	85.7
UNF 21	100.0	0.0	0.0	0.0	0.0	93.8	31.3	0.0	0.0	0.0
22	40.0	0.0	56.3	0.0	40.0	81.3	0.0	66.7	26.7	75.0
23	—	—	—	—	—	81.3	0.0	0.0	0.0	0.0
24	45.5	66.7	68.8	0.0	100.0	81.3	100.0	100.0	20.0	100.0
25	0.0	0.0	6.3	0.0	100.0	0.0	0.0	0.0	0.0	100.0
26	0.0	0.0	0.0	0.0	80.0	0.0	0.0	0.0	0.0	50.0
27	4.2	0.0	31.3	0.0	76.0	—	—	—	—	—
UNH 28	38.1	33.3	75.0	0.0	59.1	93.8	62.5	50.0	100.0	100.0
29	52.4	66.7	87.5	66.7	100.0	93.8	75.0	100.0	100.0	100.0
30	28.6	33.3	18.8	16.7	77.3	62.5	75.0	0.0	6.7	100.0
31	38.1	50.0	12.5	0.0	95.5	68.8	86.7	0.0	20.0	100.0
32	42.9	0.0	6.3	0.0	22.7	93.3	12.5	0.0	0.0	0.0
33	0.0	0.0	100.0	100.0	100.0	0.0	0.0	100.0	46.7	100.0
34	0.0	0.0	93.8	33.3	45.5	0.0	0.0	0.0	80.0	14.3

APPENDIX III

Classification of the hindwing border ocellus (spotting) phenotypes of *H. wyssii* in the Canary Islands

UPH Spots	Code	Spots	Code	UNH Spots	Code	Spots	Code
00000	A	12005	K	00005	01	12300	12
00005	B	02345	L	$0000\underline{5}$	02	12305	13
$0000\underline{5}$	C	$0234\bar{5}$	M	02005	03	$1230\underline{5}$	14
$0000\bar{5}$	D	12045	N	$0200\underline{5}$	04	12045	15
00045	E	$1204\bar{5}$	O	10005	05	$1204\underline{5}$	16
02005	F	12345	P	00045	06	02345	17
$0200\bar{5}$	G	$1234\bar{5}$	Q	12005	07	$0234\underline{5}$	18
02045	H	$1234\underline{5}$	R	$1200\underline{5}$	08	$0234\bar{5}$	19
$0204\underline{5}$	I			02045	09	12345	20
$0204\bar{5}$	J			02305	10	$1234\underline{5}$	21
				00345	11	$1234\bar{5}$	22

Spots are numbered antero-posterially from the costal side as follows : 1 (s6), 2 (s5), 3 (s4), 4 (s3), 5 (s2). White pupils are indicated as e.g. $\underline{5}$ and yellow halos as e.g. $\bar{5}$.

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Danaus chrysippus Linnaeus, 1758 ; a review of records and present status in the Maghreb countries of Morocco, Algeria and Tunisia (Lepidoptera, Danainae)

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Summary

Danaus chrysippus Linnaeus, 1758, was first reliably noted from Algeria in 1912, from Morocco in 1943 and from Tunisia in 1952 ; it has since been recorded there sporadically. Sightings have increased in recent years and some have wrongly been claimed as new country records, due possibly to the erroneous claim in early editions (and English language editions/reprints up to 1993) of Higgins & Riley's "Field guide to the butterflies of Britain and Europe" that the species had not been recorded from Algeria or Tunisia. Known records of *Danaus chrysippus* in the Maghreb countries of Morocco, Algeria and Tunisia are reviewed here. It is shown that the butterfly has established breeding populations in all three countries. Hostplants are discussed.

Résumé

Danaus chrysippus Linnaeus, 1758, fut signalé pour la première fois d'Algérie en 1912, du Maroc en 1943 et de Tunisie en 1952 ; il a fait l'objet, depuis, de citations sporadiques. Les observations se sont multipliées ces dernières années, dont certaines indûment revendiquées comme nouvelles, censément en raison de l'assertion erronée des premières éditions (et éditions en langue anglaise, réimprimées jusqu'en 1993) du «Guide des Papillons de Grande-Bretagne et d'Europe» de Higgins & Riley, donnant l'espèce comme inconnue d'Algérie ou de Tunisie. Les citations de *Danaus chrysippus* des pays maghrébins du Maroc, d'Algérie et de Tunisie sont ici rassemblées. Il est démontré que le Petit Monarque a établi des colonies stables dans ces trois pays. Les plantes-hôtes sont étudiées.

Zusammenfassung

Danaus chrysippus Linnaeus, 1758, wurde aus Algerien erstmals 1912 gemeldet, aus Marokko 1943 und aus Tunesien 1952 ; seitdem wurde er dort sporadisch gesichtet. In den letzten Jahren häuften sich die Beobachtungen ; dabei wurden einige fälschlich als Erstnachweise bezeichnet. Dies ist vermutlich darauf zurückzuführen, daß in früheren Ausgaben des Feldführers „Die Tagfalter Europas und Nordwestafrikas“ von Higgins und Riley irrtümlich behauptet wird, die Art sei aus Algerien oder Tunesien nicht bekannt. Die bisher bekannten Nachweise von *Danaus chrysippus* in den Maghreb-Ländern Marokko, Algerien und Tunesien werden zusammengestellt. Es wird gezeigt, daß der Falter in allen drei Ländern bodenständige Populationen besitzt. Die Futterpflanzen werden diskutiert.

Introduction

There has been some confusion in recent years over the occurrence and distribution of the butterfly *Danaus chrysippus* Linnaeus, 1758, in the Maghreb states of Morocco, Algeria and Tunisia. Higgins & Riley, in all English language editions to date of their Field Guide to the Butterflies of Britain and Europe, currently the only guide to the region, stated that the butterfly is a rare migrant in Morocco and has not been reported from Algeria or Tunisia. The most recent French language edition is more up to date.

A mass of further information has been published, in a number of languages in a variety of entomological journals, on the distribution of *D. chrysippus* in the Maghreb and in Europe with some recent papers claiming new records for Algeria and Tunisia. There has also been speculation and discussion on the probable hostplants of *D. chrysippus* in North Africa.

This paper sets out to collate published records to date ; to assess the present status of the butterfly in the Maghreb and to identify hostplants in each country. All localities can be found on the map (Fig. 1). Whilst the occurrence of *D. chrysippus* in Europe is outside the scope of this paper, it has been seen more frequently there in recent years and published records noted are included in the form of a bibliography.

Records to date

(M) = Morocco ; (A) = Algeria ; (T) = Tunisia

1905 — Joannis (1908 : 83), in his list of Saharan Lepidoptera recorded by Chudeau on a voyage from Algiers to Timbouctou in 1905-6, noted *D. chrysippus* 'var.' *alcippus* Cramer, 1777 taken at Oued Kadamellet on 21 September 1905 and as this has been quoted (including by the present author !) as the first published record of *Danaus chrysippus* in Algeria, it is worth taking a moment to establish where Kadamellet lies. It transpires that the locality is in Niger.

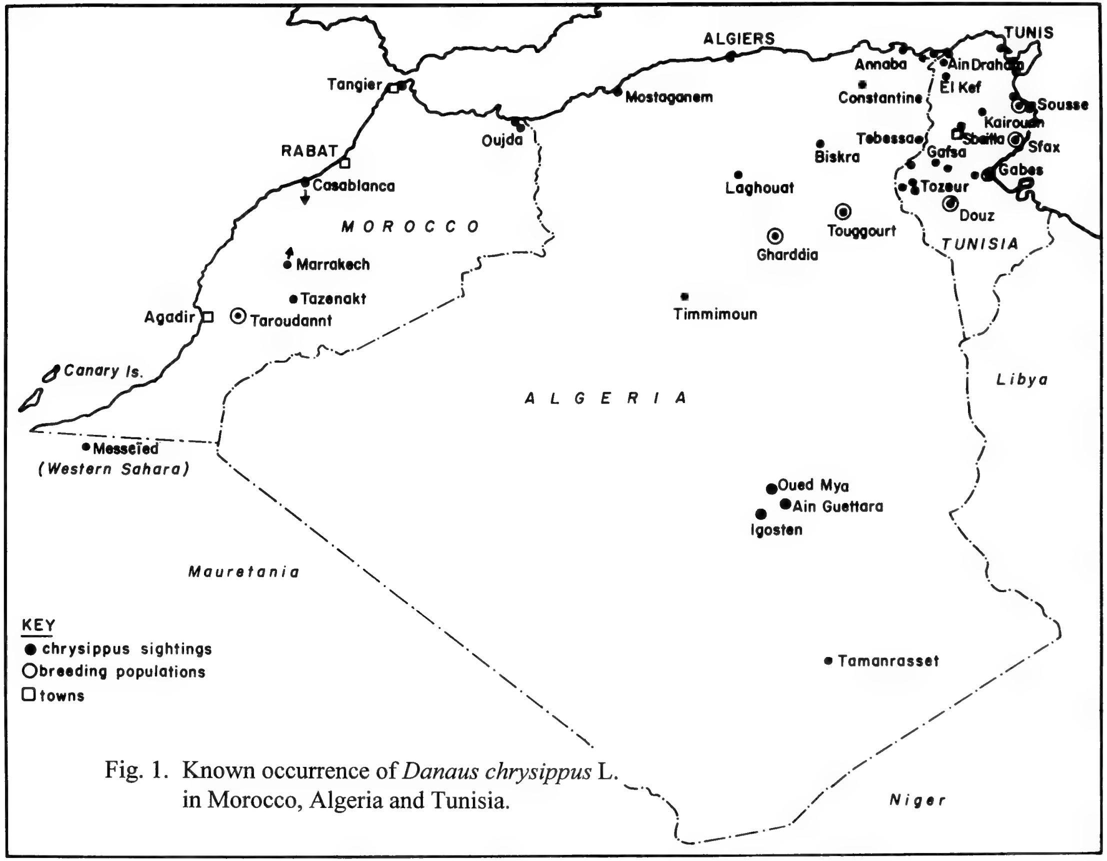

Fig. 1. Known occurrence of *Danaus chrysippus* L. in Morocco, Algeria and Tunisia.

The author was unable to find reference to Oued Kadamellet on any modern map. However, Mont Kadamellet was eventually identified on a very old map at 19° 34′ N, 8° 36′ E, some 45 km NNE of Iferouane, Aïr, the position loosely described by Joannis (1908 : 82). In June 1905, an agreement between the Commandant of what was then Haut Sénégal et Niger and the military commander of the Department de l'oasis (part of Territories du Sud Algerien), determined a boundary between Algeria and French West Africa which was completed in principle by the Niamey Conventions of 1909 (International Boundary Study No. 99). Thus 'Kadamellet' was and is in Niger, about 200 km SE of the Algerian border.

1907 — Seitz (1907 : 75-76), noted that [form] *chrysippus* was to be found on the Canary Islands "and the opposite districts of Morocco ... The absence of the insect from Algiers [Algeria] is very remarkable ... ab. *alcippoides*... in the Palearctic region only on the Canaries and in the opposite districts of Morocco ...". The source of these comments is not clear ; there are no *D. chrysippus* from N Africa in the Seitz collection, now in the Senckenberg Museum, Frankfurt am Main (H. Schroeder, pers. comm.)

1912 — Rothschild (1913 : 114), recorded a male specimen from South Oued Mya (A) [30 April 1912] (another was seen but not captured) ; a female north of Aïn Guettara (A) [8-11 April 1912] and a male from Igosten, Tidikelt (A) [15 April 1912] among the butterflies collected by Hartert in an expedition to the central western Sahara. He correctly noted these specimens as the first records for Algerian territory. The specimens remain extant in the Rothschild collection at the BM(NH).

1923 — Demaison (1923 : 134) reported his brother finding a single f. *alcippus* at Ghardaia (A) on 22 April 1923 and seeing several more on subsequent days in the same place. His brother also apparently found it commonly at Touggourt oasis (A) on 1 May 1923. In April 1927 Demaison's brother returned to Ghardaia but saw no further specimens (Demaison, 1932 : 93), prompting Demaison to suggest that its occurrence in large numbers in the area in 1923 was due to an "accidental migration". Apparently all individuals seen then were f. *alcippus*. He mentioned *Gomphocarpus fruticosus* (Asclepiadaceae), a known hostplant of *D. chrysippus* (Ackery & Vane-Wright, 1984 : 210), as a possible hostplant there.

1943 — Rungs (1945 : 15) noted 6 examples of f. "*kanariensis*" Fruhstorfer, 1898, [a doubtfully distinct race essentially of the "*chrysippus*" form (Ackery & Vane-Wright, 1984 : 115)], and one f. *alcippus* at

Messeïed, Rio de Oro in SW Morocco (Western Sahara), taken on 20 January 1943 by Morales Agacino who observed further adults and larvae associated with *Calotropis procera* (Asclepiadaceae).

1947 — Rungs (1950 : 144-5) stated that despite much travelling in southern Morocco, he failed to find *D. chrysippus* until December 1947 when he found all stages of the insect abundantly some kilometres west of Taroudannt (M) ; of 38 specimens taken, only 6 were f. *alcippus*, the remainder being "f. *kanariensis*" [*chrysippus*] or *alcippoides*. The hostplant was *Asclepias curassavica* f. *atropurpurea* (Asclepiadaceae) ; Rungs expressed surprise at the apparent rarity of *D. chrysippus* in view of the availability of a number of different and presumably quite suitable Asclepiad hostplants.

1952 — Chnéour (1953) recorded Bede telling him that it was to be found frequently in the Biskra and Ghardaia areas of Algeria and that Kruglik had observed it in some numbers at Nefta (T). He recorded the capture, by Demoflys, of a single f. *alcippoides* at Gabès (T) on 4 July 1952. He added that since the time of this first observation, other specimens had been seen at Tozeur (T), Aïn Draham (T) and Mégrine (T) (by Chpakowsky) and at Barrage de l'Oued Kebir (T) (by Massal and Arnould). This record was repeated (Chnèour, 1954 : 222) and the butterfly was depicted on the front cover of volume 7 of Bull. Soc. Sci. nat. Tunis.

1956 — Wyatt (1956 : 220) recorded the species in the Sous valley (Taroudannt) (M) and noted that approximately 30% of individuals seen were f. *alcippus*.

1970 — Higgins & Riley, in their Field Guide to the Butterflies of Britain and Europe, stated that *D. chrysippus* was a rare migrant in Morocco and not reported from Algeria or Tunisia ; claims reiterated in subsequent English language editions (1973, 1975, 1980, 1983) and reprints up to 1993. The French language edition of 1988, the only one the author has examined, went some way to correcting these mistakes.

1971 — Owen (1971 : 138 [Fig. 9.2]), included all of Tunisia and most of Algeria and Morocco well into the Sahara desert in the distribution of f. *chrysippus* in Africa. He showed f. *alcippus* occupying most of Morocco and part of western Algeria, far removed from the extensive populations of western Africa and went on to say (1971 : 140) that maps were prepared after examination of the large collections in the British Museum [Natural History] and in the Hope Department of Entomology at Oxford. This is puzzling since the author was unable to find any *D. chrysippus* from N Africa other than from Egypt, Libya and Mauretania and those recorded by Rothschild in 1912 in the BM(NH) collections, or in the Hope Department of Entomology at Oxford University Museum. A number of specimens from Morocco and Tunisia have been deposited by the present author in the BM(NH) collection.

1971 — Kudrna (1972 : 268) recorded the capture by Gawadi and Wilson on 1 September 1971 of 1 male and 3 females at Taroudannt (M) where it was common and fresh, having apparently bred locally.

1974 — Pierre (1974) provided comprehensive discussion on the distribution of *D. chrysippus* throughout Africa and included parts of Algeria in the distribution of f. *alcippus*, as well as including W Moroccan and S Algerian records of f. *chrysippus*. This was based on a number of specimens in the collections of the Museum National d'Histoire Naturelle in Paris, namely Alger, Maison Carée (1, ex. Balachowski — *alcippus*) ; Touggourt (A) (5, ex. Babault — *alcippus*) ; Ghardaia (A) (1, ex. Demaison — *alcippus*) and Timmimoun (A) (1 *chrysippus*) (J. Pierre, pers. comm.)

1975 — Samraoui (1993 : 69) noted a specimen captured in Tebessa (A) in 1975, in the INVP collection in Algiers.

1979 — Devarenne (1981 : 171) recorded it in March and September/October 1979 around Ghardaia (A) and figured an extreme male aberration taken in October of that year.

1979 — de Friena (1981) recorded Menrad taking a series at Sousse (T) on 16 December 1979, some of which were f. *alcippoides* ; he also discussed several possible hostplants.

1979/80 — Schuurmans (1981) found *D. chrysippus* at Sousse (T) in 1979 and recorded Myncke finding it commonly from the beginning of August until mid-October at Monastir (T), Sousse (T) and Jendouba (T).

1980 — Lempke (1981 : 35) recorded a specimen at Sousse (T) on 2 March 1980.

1980 — van Cappellen (1981) illustrated a female specimen found by Bolland on 11 March 1980 at Sousse (T).

1980 — Lüttgen (1981 : 55) found two examples of the nominate form at Tozeur (T) on 4 October 1980.

1980/1981 — There are specimens in the Museum National d'Histoire Naturelle, Paris, from near Sbeitla (T) (7, Ex. Barbery & Aubertin, 1980/81 — *chrysippus*) ; R. Lheureux apparently also observed 3 specimens at Béthioua (A) and Mostaganem (A) in 1980 (J. PIERRE, pers. comm.)

1982 — BURTON (1982) mentioned several hundred *D. chrysippus* seen by Tombs in the region of Monastir (T) and Sousse (T) from 6 to 10 June 1982.

1983 — CASSAR (1983) noted a total of 19 specimens on 10 and 13 July 1983 near Kairouan (T), La Kesra (T) and El Kef (T).

1985 — Between 12 and 24 June 1985, LEGLER (1986) saw a number of specimens in the area of Hammamet (T).

1985 — DEVARENNE (1990 : 154) reported it as common in various localities in Tunisia ; all stages of the butterfly were found in May 1985 between Sousse (T) and Port-el-Kataoui (T) feeding on *Pergularia tomentosa* (Asclepiadaceae). The butterfly was seen in "almost every part of Tunisia, including Tunis".

1985/6 — CASSAR (1989) reported a single specimen seen by Balzan at Tunis (T) on 9 April 1985 and scores seen at Douz (T) in early October 1986. He went on to report a male specimen on 9 October 1986 at Touggourt (A) ; this last record was believed to be the first for Algeria.

1988 — HÜNI (1988) saw the species near El Djem (T) and Sidi Bou Ali (T).

1988 — STEINIGER & EITSCHBERGER (1990 : 169), noted a specimen seen to the east of Tangier (M) on 25 October 1988.

1990 — SAMRAOUI & BENYACOUB (1991) observed a build up of *D. chrysippus* apparently migrating from east to west in the region of Annaba (A) and El-Kelaa (A) in May 1990 ; the last specimen seen in Annaba was on 17 October. On 27 August 1990 about 20 specimens were seen at Touggourt (A), also apparently moving in an east/west direction.

1990 — Observed to be widespread in small numbers beween Casablanca and Marrakech (M) on 3 October 1990 ; also seen near Tazenakht, 60km SW of Ouarzazate (M) on 11 October 1990 (Martin Jacoby, pers. comm.).

1991 — SAMRAOUI *et al.* (1992) noted the butterfly at Lac Bleu (A) (2) on 28 May 1991, El-Chatt (A) (1) on 14 June 1991, Lac des Oiseaux (A) (1) on 21 June 1991, Biskra (A) (numerous) on 19 July 1991, Laghouat (A) (numerous) on 26 July 1991, Ghardaia (A) (numerous) on 28 July 1991, Touggourt (A) (3) on 5 August 1991 and Tamanrasset (A) (1) on 10 October 1991. *Calotropis procera* (Asclepiadaceae) was suggested as a probable hostplant in central and southern Algeria.

1991 — 1 example was seen at the Gorges de Zeghzel, Berkane (M) on 28 September 1991 and about 15 specimens at the Moulouya delta (M) on 9 October 1991 by G. Chavanon (H.-J. Falkenhahn, pers. comm.).

Author's observations 1991-1993

MOROCCO : On 11 September 1991, a few individuals were seen in different localities on the eastern and northern outskirts of Taroudannt. The following day quite large numbers (40-60) were seen west of the town where there was a large stand of *Asclepias curassavica* growing in an irrigation ditch (Tennent, 1993 : 27). On 3 March 1992 the area was revisited when it was found that the irrigation ditches had been cleared of all "debris", including *curassavica* plants ; only a single *D. chrysippus* was seen to the east of Taroudannt. On 11 May, four specimens were seen in close proximity to *curassavica* plants at Ait Iazza, east of Taroudannt and on 4 June, a single example was seen flying across the main road 24 km east of the town. A further specimen was seen just south of Taroudannt on 2 September, the last visit of that year.

In 1993, the locality west of Taroudannt where both the butterfly and hostplant were common in the autumn of 1991,was visited on 26 May. Although *curissavica* had begun to repopulate the ditch, individual plants were very small and no *D. chrysippus* were seen. However, at Ait Iazza, both the plant and the butterfly were quite common ; with about 20 butterflies observed in a half hour period.

Of *D. chrysippus* butterflies seen in Morocco, some 60-70% were of the nominotypical form, with the remainder being f. *alcippus* or *alcippoides* ; the latter were very variable, displaying a white hindwing patch of variable size or merely a few white scales around the inner margin.

The author travelled extensively in Morocco in 1992 and 1993 but never saw *D. chrysippus* other than around Taroudannt and the Sous river valley. It was seen on each visit to the area, even when merely "passing through" ; individuals appeared generally to be freshly emerged.

ALGERIA : From 15-17 March 1992, small numbers of *D. chrysippus* (about 10 in total) were seen close to the town of Ghardaia in central Algeria. Some individuals were possibly in transit, but others appeared settled in an area west of the town where *Pergularia tomentosa* (Asclepiadaceae) grew commonly. A few *Asclepias curassavica* plants seen incorporated in a display along the central reservation of a street on the outskirts of Berriane, 40km north of Ghardaia, were thickly covered in dust ; no *D. chrysippus* were seen. It was not seen at Tougourt some days later, although only a very cursory search was carried out. Two specimens were seen at Ghardaia on 3 October.

In 1993, 2 individuals were seen flying aimlessly in the centre of Tamanrasset town on 24 April and a third (or one of the previous two again ?) in the same place the following day.

A single example was seen flying across the road 34km south of Ghardaia on 1 May. The very small entomological collection at the Institut National de la Protection desVegetaux in Ghardaia contains only three butterflies — 2 male *D. chrysippus* and 1 male Pieris rapae Linnaeus, 1758 (identified as *P. napi* !) ; according to an official of the Institute, *D. chrysippus* is a regular visitor to the Institute gardens.

Without exception, butterflies seen by the author in Algeria have been of the nominotypical form.

TUNISIA : On 4 October 1992, single specimens were seen at Degache and Tozeur ; the butterfly was very common in an oasis on the southern outskirts of Douz, about 150 individuals were seen in one afternoon including seven pairs in copula. Two larvae were noted on (?) *Cynanchum* sp. (Asclepiadaceae). One freshly emerged male f. *alcippus* was seen ; the remainder of those seen at Douz and subsequently elsewhere in Tunisia, were f. *chrysippus*. On 5 October it was also common (including one pair seen in copula) in cultivated areas on the western outskirts of Gabes ; the following day two were seen flying in Gabes town centre and singletons seen at Oudre ; in the desert 42km west of Gabes ; El Guettar and Gafsa. On 7 October it was flying quite commonly in a dry river bed on the outskirts of Moulares and 3 days later, three were seen ca. 30km north of Sbeitla.

In 1993, a year when the Spring season was delayed, one *D. chrysippus* was seen on the eastern outskirts of Gafsa and another near El Guettar on 30 March ; on 5 April a single specimen was seen at Douz.

In October 1992, at the Institut National Agronomique de Tunisie (INAT) in Tunis, a display case containing preserved stages and host-plant (*Pergularia tomentosa*) of *Danaus chrysippus* was seen in the foyer of the zoology department, apparently prepared by Monsieur Hédi Smiri, an amateur lepidopterist working at the Institut National de la Recherche Agronomique de Tunisie (INRAT) in Sfax. On 23 March 1993 the author met Monsieur Smiri who confirmed that he had been breeding *D. chrysippus* regularly during the previous ten years from early stages found locally ; a search failed to find any pupae, the only stage we might have expected to see since the butterfly had not yet emerged that year.

Present Status

Danaus chrysippus is a strongly migratory butterfly, with individuals often wandering far from established colonies. However, there is strong evidence that the species has established breeding colonies in Morocco, Algeria and Tunisia within the last 50 years.

MOROCCO : *Danaus chrysippus* is clearly well established in the Sous valley, where it has almost certainly been resident since 1947 or earlier. It seems likely that the Morocco populations originated from western Africa ; forms *alcippus* and *alcippoides* form a significant percentage of the population.

Although other Asclepiads are available, particulary in the south of the country, the only confirmed hostplant utilised by *D. chrysippus* in Morocco is *Asclepias curassavica*, introduced into Africa as a garden plant from Tropical America (Owen, 1971 : 34). The plant, which grows as a weed on the edges of fields and irrigation ditches around Taroudannt, seems to be irregularly but routinely destroyed by the local farmers and this probably has a direct bearing on the fluctuation of the *D. chrysippus* population. The botanist J. Gattefossé appears to have been the first to find *curassavica* in the Taroudannt area of Morocco in 1940 (Gattefossé, 1941 : 214).

ALGERIA : It is interesting that the "invasion" of *D. chrysippus* to the Ghardaia and Touggourt areas recorded by Demaison in 1923 consisted exclusively of f. *alcippus*, whereas those seen in recent years have all been (where recorded) of the nominate form. Clearly, the butterfly has established for some years a breeding population at Ghardaia and Touggourt and probably elsewhere in that region.

The hostplant(s) in Algeria is not clearly established. However, with the exception of Tamanrasset where the butterflies were seen only in the town centre, the asclepiad *Pergularia tomentosa* was present, usually commonly, in every locality where the author observed the butterfly. It seems likely therefore that this is the hostplant, though not necessarily the only one. *Calotropis procera* and other *Calotropis* species (Asclepiadaceae) have been suggested as hostplants although, if that were so, one might reasonably expect *D. chrysippus* to be more common and widespread than it is in Algeria, since *procera* is a very common plant in the desert. It is a hostplant of *D. chrysippus* in West Africa (VAN DER HEYDEN, 1992).

TUNISIA : The butterfly is a notable vagrant and the relatively numerous records from various parts of Tunisia in the last 15 years may herald a spread in distribution from those areas of southern Tunisia (Sfax, Gabes, Douz etc.) where it appears to have been resident for some years. Although occasional individuals of f. *alcippus* occur, the resident form is apparently nominotypical like that to the west in east central Algeria.

The primary hostplant in coastal Tunisia, including Sfax, Gabes etc., is *Pergularia tomentosa,* not recorded amongst the more than 50 Asclepiadaceae hostplants for *D. chrysippus* listed by ACKERY & VANE-WRIGHT (1984 : 210-211). At Douz, the hostplant seems to be a (?) *Cynanchum* species ; the number of other possible asclepiad hostplants in Tunisia makes it quite likely that other species are also utilised.

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Further notes on *Berberia* de Lesse species in North Africa and confirmation that *B. abdelkader* Pierret, 1837 and *B. lambessanus* Staudinger, 1901 are significantly distinct (Lepidoptera, Satyridae)

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Summary

Subsequent to the author's previous work on the genus *Berberia* de Lesse in NW Africa (Tennent, 1994), in June 1994, a mixed population of *B. abdelkader* Pierret and *B. lambessanus* Staudinger was discovered flying in the Moroccan High Atlas mountains. A number of male butterflies were secured, all of which were clearly identifiable as either *abdelkader* or *lambessanus*. The probable hostplant was identified as *Stipa parviflora*.

Résumé

Après la publication de son article sur le genre *Berberia* de Lesse en Afrique du Nord occidentale (Tennent, 1994), l'auteur a découvert en juin 1994 une population mixte de *B. abdelkader* Pierret et *B. lambessanus* Staudinger qui volaient ensemble dans le Haut-Atlas marocain. Il a capturé une série de mâles dont tous étaient nettement identifiables comme *abdelkader* ou *lambessanus*. La plante nourricière des chenilles a été déterminée : *Stipa parviflora*.

Zusammenfassung

Nach der Publikation einer früheren Arbeit über *Berberia* de Lesse in Nordwestafrika (Tennent, 1994) wurde im Juni 1994 im marokkanischen Hohen Atlas eine gemischte Population von *B. abdelkader* Pierret und *B. lambessanus* Staudinger entdeckt. Alle gefangenen Männchen ließen sich eindeutig als *abdelkader* oder *lambessanus* bestimmen. Futterpflanze ist vermutlich *Stipa parviflora*.

This short paper should be considered in conjunction with the author's previous work on *Berberia* de Lesse (Tennent, 1994). Since preparing that paper in 1992, further lengthy visits have been made to the Maghreb, particularly Morocco, and on 8/9 June 1994, at 2150-

2250 metres on the shores of Lac Tislit (Imilchil) in the Moroccan High Atlas mountains, a mixed population of *Berberia abdelkader abdelkader* Pierret and *B. lambessanus* Staudinger was discovered.

In raising *B. lambessanus* to specific status, the author ventured the opinion (Tennent, 1994 : 314) that *B. abdelkader* and *B. lambessanus* were unlikely to be found flying together because of (presumed) differing biological requirements. The Tislit biotope consists primarily of extensive stands of *Stipa parviflora* grass (det. Mr. Roy Vickery, Dept. of Botany, BM(NH)), which presumably serves as the hostplant for both species. Neither species was particularly common. Most individuals were seen on a steep rocky slope where pursuit was difficult and in two days a total of 24 males and 1 female were secured ; collection was arbitrary, many more were seen than taken and it proved impossible to accurately determine identity in flight. The males comprised 20 (83%) typical *abdelkader* and 4 (17%) typical *lambessanus* ; the single female was tentatively placed as *B. abdelkader*.

There are two possible explanations for the discovery of *abdelkader* and *lambessanus* flying together. Firstly, that *abdelkader* is a dimorphic (polymorphic if *nelvai* Seitz and *taghzefti* Wyatt are included) species or secondly, since by definition no two 'subspecies' of the same form may fly together, that two separate species are involved. The first explanation may reasonably be discarded, since all other known populations are almost exclusively of one "form" or the other and their respective hostplants are different (Tennent, 1994 : 303, 314). Having said that, it is true that *lambessanus*-like forms occur rarely in *abdelkader* populations, and very infrequent specimens of *lambessanus* transitional to *abdelkader* were noted by the author in 1993 in the western Rif mountains and on Djebel Aourach, NE of the Dades gorge ; a circumstance not unexpected in such closely related taxa.

Of the Lac Tislit material examined, most were fresh and all males were clearly of one form or the other, with the upperside ground colour of *lambessanus* very dark brown, almost black and that of *abdelkader* dark chocolate-brown with the forewing apical ocellus ringed completely or partly by pale scales. Females of both species are generally difficult to separate. On balance, *abdelkader* from Tislit had a dark overall appearance compared with other populations, although many individuals were indistinguishable from those taken by the author in several localities in Algeria.

Apart from the obvious interest in finding *abdelkader* and *lambessanus* flying together, the occurrence of typical *abdelkader* in southern Morocco, some 380 km SW of the nearest previously known population, is equally interesting and raises further questions as to the status of *B. abdelkader nelvai* and *B. abdelkader taghzefti*. One might have expected *abdelkader* flying in the northern High Atlas to be *B. a. taghzefti*, the nearest known population of which flies on the Tizi-n-Tairhemt in the extreme NE of that range (wrongly recorded by the author as being in the Middle Atlas mountains (TENNENT, 1994 : 308, 309)), a little more than 100 km NE of Lac Tislit. In preparing the previous paper, the author believed that a case may be made for considering *nelvai* a good species, based on its distinctive appearance, unusually late flight period, apparently clear geographical parameters and the fact that typical *abdelkader* flies both to the west and (from the small number of specimens in the BM(NH) collection in London from the Gharyan hills in W Libya) to the east. Although the evidence was deemed inconclusive, finding typical *abdelkader* in S Morocco lends support to this view since *nelvai* and *taghzefti* are in effect surrounded both by typical *abdelkader* and *lambessanus*.

Clearly, still more work needs to be done to finally resolve this interesting problem ; sadly the declaration by the FIS in September 1993 that foreigners in Algeria were considered a legitimate target, and the subsequent killing of many Europeans there, makes travel in that country in the foreseeable future impossible.

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Short communication — Kurze Mitteilung — En bref

***Pempeliella ornatella* (D. & S.) et *Actinotia hyperici* (D. & S.), espèces nouvelles pour la Seine Maritime (Normandie, France) (Lepidoptera : Pyralidae, Pterophoridae, Noctuidae)**

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Dans la nuit du 26 au 27 juin 1992, nous avons installé notre lampe à vapeur de mercure au pied d'une colline de sable (dune fossile ?) située à l'Ouest de Notre Dame de Gravenchon (Seine Maritime), le long de la route D 928 (UTM CQ28). Les pentes sont occupées par une garenne dont la végétation diffère notablement des biotopes des coteaux calcaires de la région et sont couronnées de taillis de *Prunus, Crataegus* et *Salix.* Notre observation s'est déroulée dans la deuxième partie de la nuit de 0h45 à 2h30 (heure légale).

Quelques microlépidoptères se sont ajoutées aux 60 espèces de macrolépidoptères observées et parmi eux *Pempeliella ornatella* (D. & S.) qui était demeurée inconnue de Seine Maritime. D'après le catalogue de L. Lhomme (1935-1949 : 21), la chenille de cette pyrale se nourrit aux dépens de *Thymus serpyllum*, plante répandue dans le lieu visité (*Thymus drucei* en Angleterre ; Goater, 1986). Nous remercions le Dr. M. Laine pour la détermination de ce Phycitinae, qu'il avait signalé de l'Eure dans son catalogue (1986) d'après une capture de L. Dupont.

Nous avons également pu capturer un exemplaire mâle très frais de *Actinotia hyperici* (D. & S.), Noctuidae nouvelle pour la Seine Maritime et connue depuis peu dans l'Eure (Sauvagère, 1989). La localité de Notre Dame de Gravenchon paraît être la plus septentrionale pour cette espèce dans le Nord Ouest de la France.

Ce biotope recèle également un Ptérophore peu signalé en Normandie : *Stenoptilia zophodactyla* (Dup.) ; 2 ex. le 27-VI-1992 et 2 ex. le 21-VIII-1993.

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Helsinki April 19-23, 1992

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Population biology of *Proclossiana eunomia* : Preliminary results on morphometric and allozyme variation in Belgian and French populations (Lepidoptera, Nymphalidae)

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Summary

Samples of *Proclossiana eunomia* (Esper, 1799) from Belgium and France were analysed by protein electrophoresis and morphometrics. The population from Morvan, central France, where the species was introduced from the Ardennes, is morphologically distinct from its mother population and has lost some alleles, due to a foundation effect. The within-region difference is usually small compared with between-region differences. The validity of the Pyrennean subspecies *P. eunomia ceretanensis* Deslandes, 1930 is confirmed.

Résumé

Des échantillons de *Proclossiana eunomia* (Esper, 1799) de France et de Belgique ont été analysés par morphométrie et électrophorèse des protéines. La population du Morvan, où l'espèce a été introduite depuis les Ardennes, est morphologiquement distincte et a perdu des allèles suite à un effet de fondation. Les différences au sein des régions sont en général plus faibles que celles entre les régions. La validité de la sous-espèce pyrénéenne *P. eunomia ceretanensis* Deslandes, 1930 est confirmée.

In Belgium, 81 of the 120 native species of Rhopalocera have shown a significant shrinking of their distribution this century (Baguette *et al.*, 1992). More than half of the Belgian butterfly species are threatened, being in the "endangered", "vulnerable", "rare" or "indetermined" IUCN classes of vulnerability (Baguette & Goffart, 1991). The species more prone to decline are those with strong ecological requirements, and often are linked with specific semi-natural habitats. To address concerns about the future of the declining species, one needs information, not only of their distribution and habitat requirements, but also of their genetic diversity (FRANKEL & SOULÉ, 1980 ; ALLENDORF, 1983 ; TEMPLETON, 1991).

In order to investigate how this distribution decline may affect the survival of the concerned species, genetic studies have begun independently in France and in Belgium in 1991 on *Proclossiana eunomia* Esper. This species has a very restricted habitat in western Europe : it is found in bogs and unfertilised wet meadows where its only local host plant *Polygonum bistorta* grows (HACKRAY & SARLET, 1969 ; DESCIMON, 1976). The patchiness of this habitat may be seen at different scales, being due both to natural and human factors. Large formerly suitable areas have frequently been fragmented by spruce (*Picea abies*) plantations or by intensively managed and fertilised pasture lands. The local abundance of *P. eunomia* and its strong habitat requirements make this species a good model to investigate how natural and man-made patchiness may influence the genetic structure of natural populations.

How genetically distinct different populations are, and how organised this variation is, are the main themes of our research. The population genetics of *P. eunomia* is currently being studied at different levels : local (within populations, within localities), regional (within regions), and between regions (within the European range of the species). Moreover, as new populations were founded in Morvan in 1970 and 1973, in an area where *P. eunomia* was hitherto absent (DESCIMON, 1976), the genetics of these populations are investigated and compared with the population of origin of the founder individuals.

Methods

P. eunomia specimens were collected in 1991 in the French Pyrenees, in the two localites where it had been introduced in Morvan (central France), in various localities in Gaume (Southern Belgium) and in the Belgian and French Ardennes, including the locality of origin of the individuals which founded the Morvan populations (Fig. 1). A sample of 206 specimens collected in Morvan in 1977, and in the French Ardennes and the Pyrenees prior to 1991 by H. Descimon was added to the morphometric analysis.

Specimens collected in the field were deep frozen in liquid nitrogen (–196° C) as soon as possible, and kept so until analysis. When thawed in the laboratory, the wings were kept for morphometric analysis, and the body was squashed in a pH 7.1 buffer (15% (w/v) sucrose, 50 mM Tris/HCl pH 7.1, 0.5% (v/v) Triton X-100, drop of Bromophenol Blue as runner marker ; WYNNE & BROOKES, 1992). Barascud followed the electrophoresis techniques described by PASTEUR *et al.* (1987), using horizontal starch gel electrophoresis, and Nève used cellulose acetate electrophoresis methods following RICHARDSON *et al.* (1986) and WYNNE *et al.* (1992). Among various allozyme loci studied, the following proved to be polymorphic in the scored populations of *P. eunomia* : Phosphoglucose isomerase (PGI, EC 5.3.1.9), amino aspartate transaminase

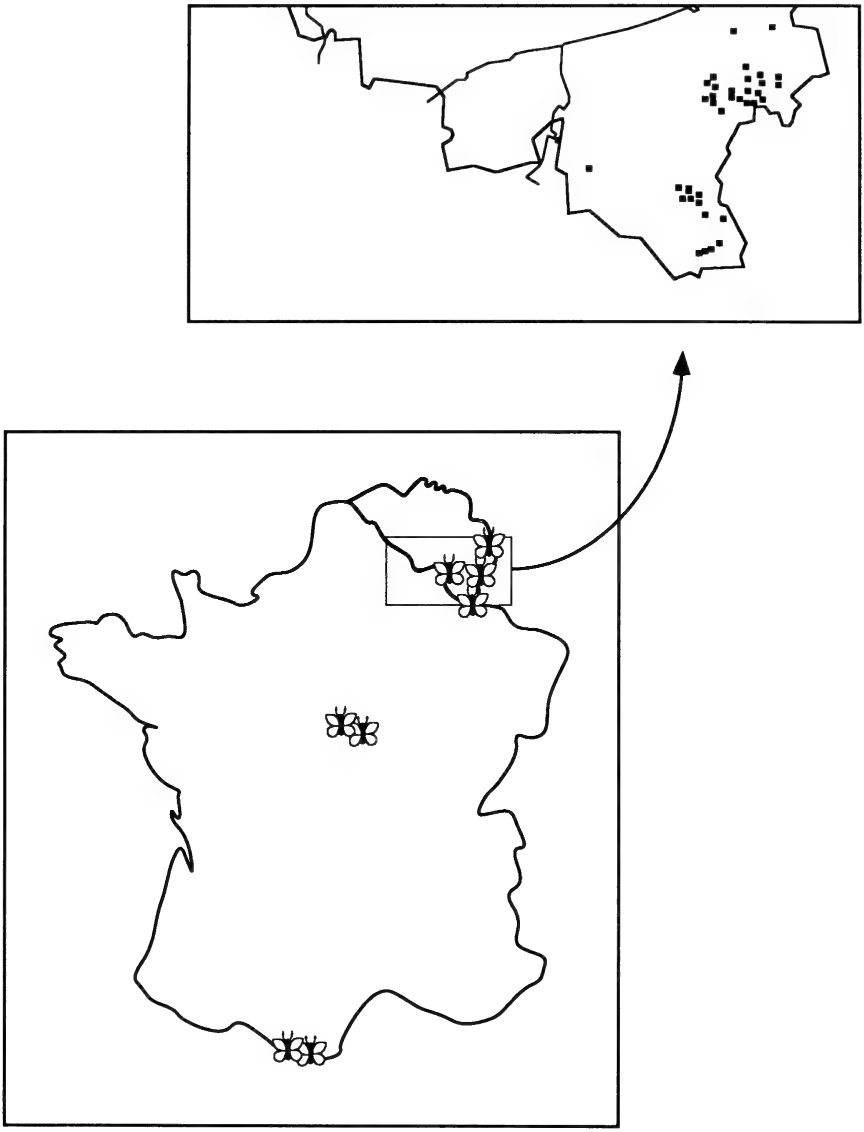
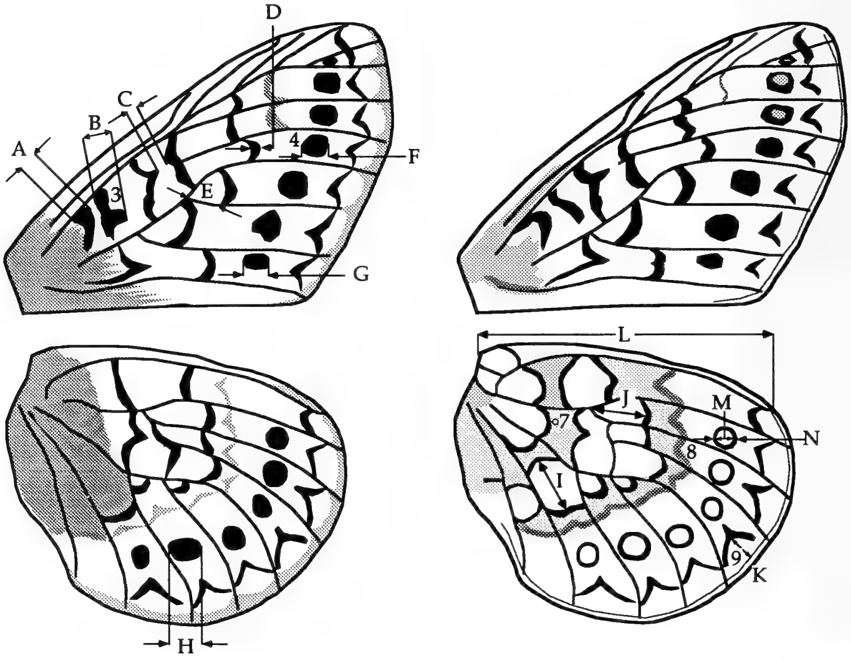


Fig. 1. Distribution of *P. eunomia* samples.

(AAT, EC 2.6.1.1), 6-phosphogluconate deshydrogenase (6PGD, EC 1.1.1.44) and phosphoglucomutase (PGM, EC 2.7.5.1).

Morphometric studies of French specimens were carried out manually, using a binocular microscope and an internal ruler to measure linear dimensions of cells and spots on the wings (Fig. 2, Table 1). For Belgian specimens, an image analyser (description and use described in Windig, 1991) was used to take measurements of surface characters (Fig. 2, Table 1). In both cases a principal component analysis was performed on a first data set where 44 and 56 characters respectively were measured on a subsample ; then a set of as few correlated characters as possible was chosen to be measured on all specimens. On the whole, 152 French and 297 Belgian specimens were collected in 1991, of which only a portion has been analysed so far.



Upperside **Underside**

Fig. 2. Wing morphometric characters.

Results

The morphometric analysis shows that regions within France are well differentiated. The two populations founded in Morvan (central France) with females from the French Ardennes in the early 1970s, already show a significant diffe-

Table 1

List of brief descriptions of morphometric characters measured.
Nomenclature of veins and cells follows HIGGINS & RILEY (1983)

French specimens

Forewing

A. Maximum width of basal black spot
B. Maximum width of discoidal black spot
C. Distance between the outer edge of the second discoidal spot and the inner edge of the median vein
D. Width of central black spot in s4
E. Distance between the connections of veins 3 and 4 and the basal edge of the spot in s3
F. Diameter of outer spot in s4
G. Diameter of outer spot in s1b

Hindwing

H. Diameter of outer spot in s2
I. Length of light "cell" in s1c
J. Distance between the connections of veins 6 and 7 and the inner side of the discal spot in s6
K. Length of submarginal light space in s4
L. "Length" of hind-wing
M. Outer diameter of eyespot in s6
N. Inner diameter of eyespot in s6

Belgian specimens

Upperside of the forewing

1. Total black surface
2. Total orange surface
3. Area of discoidal black spot
4. Area of outer spot in s4

Underside of the hindwing

5. Total black surface
6. Total orange and white surface
7. Contrast index (contrast area x contrast level) of the spot in the orange discal spot of the cell
8. Area of black outer margin of the orange spot of in s5
9. Area of submarginal light space in s4

rence from specimens of their area of origin (MANOVA analysis, $F_{14,44} = 6.36$, $P < 0.001$ for 1977 specimens, $F_{14,157} = 6.60$, $P < 0.001$ for 1991 specimens).

In order to maximise the distance between the regions, a canonical discriminant analysis was performed on the two data sets (Figs 3, 4). In France, on the first two canonical axes, a marked difference was found between the Pyrenean individuals and those from other regions. This result confirms the validity of the Pyrenean subspecies *P. eunomia ceretanensis* Deslandes, 1930. The populations from Morvan were only slightly different from Ardennean populations in 1977, but seem more so in 1991 (Fig. 3). Belgian populations are

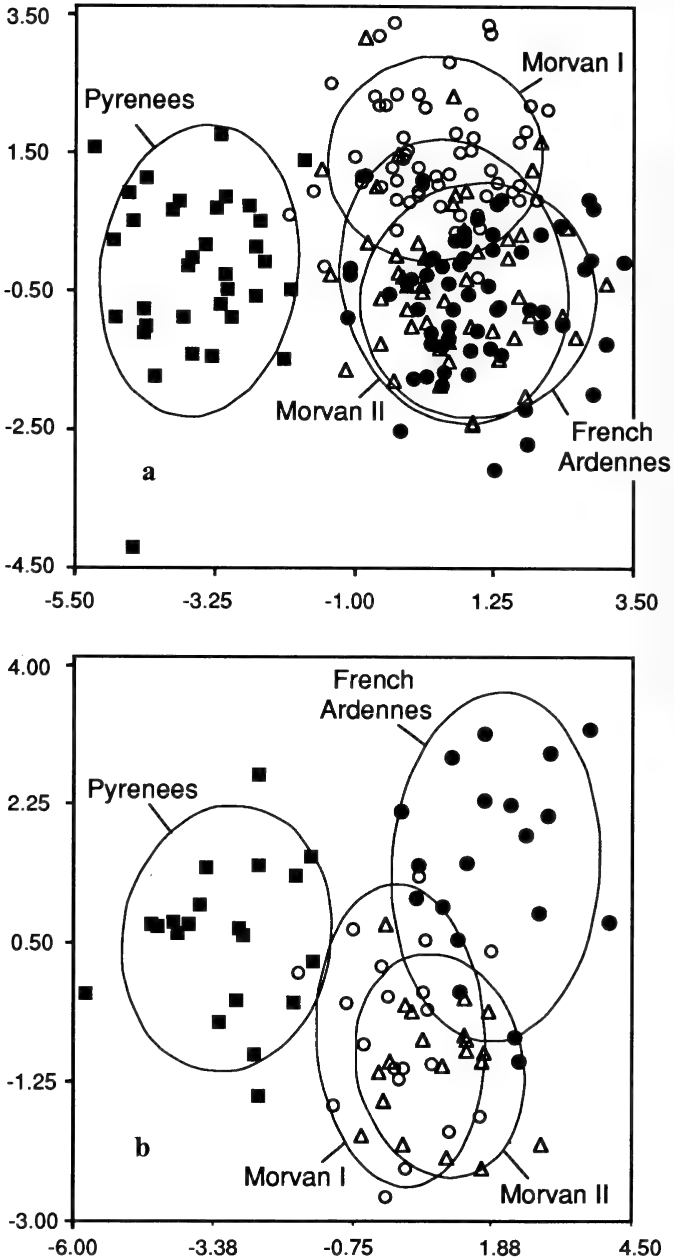


Fig. 3. Canonical discriminant analysis on morphometric characters of French specimens sampled in 1977 (Fig. 3a) and in 1991 (Fig. 3b), projection on the first two axes ; the ellipses show the 80% distribution of the samples of each group. Symbols : Pyrenees = closed squares ; French Ardennes = closed circles ; Saint Brisson (Morvan I) = open circles ; Lavault de Frétoy (Morvan II) = open triangles.

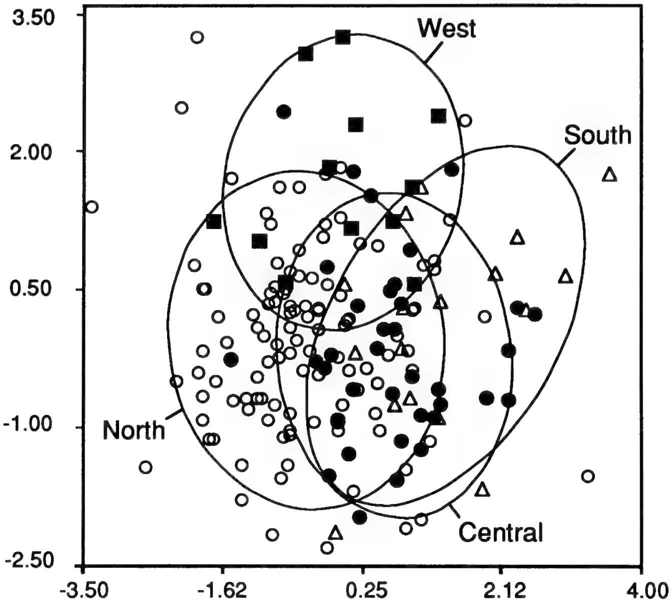


Figure 4. Canonical discriminant analysis on morphometric characters of Belgian specimens sampled in 1991, projection on the first two axes ; the ellipses show the 80% distribution of the samples of each group. Symbols : Graide (West) = closed squares ; Sûre valley (Central) = closed circles ; Plateau des Tailles and Liège Province (North) localities = open circles ; Gaume (South) = open triangles.

Table 2

Frequency of allozyme in French populations, as all studied loci are diallelic, only the frequency of the commonest allele is given. In each sample 20 individuals were scored

		Frequency of commonest allele		
Region	Locality	AAT	PGI	6PGD
Ardennes	Pont Collin	1.00	1.00	0.87
Morvan	Saint Brisson	1.00	1.00	1.00
	Lavault de Frétoy	1.00	1.00	1.00
Pyrenees	Porta	0.50	0.90	0.75
	La Tour Cerdane	0.65	0.87	0.87
	Porté	0.85	0.97	0.85

less well differentiated ; they might however display a slight North-South morphological cline (Fig. 4).

Allozyme analysis also confirms the validity of *P. e. ceretanensis*, as populations from the Pyrenees show significant differences with that from the Ardennes (Table 2). In the introduced populations of Morvan, 6PGD has lost the polymorphism present in the mother population at Pont Collin, Ardennes, indicating that the Morvan populations have suffered from a bottleneck effect.

Within Belgian populations, very low genetic differences have been observed so far, as the percentage of the commonest PGM locus varies from 72% to 81% in the 4 regions, and the difference is not significant. Too few data on other loci have been so far collected to allow any further discussion of this genetic data.

Discussion

The preliminary results of this ongoing study suggest that *P. eunomia* populations show high inter-region variation. This is not surprising, as it has been shown for other species with a disjunct distribution (e.g. *Parnassius mnemosyne* in South France, NAPOLITANO *et al.*, 1988). However, local differentiation and genetic shift of introduced populations *vs* their mother population does not rule out the possibility of selection, which has been proven to occur on the PGM locus in *Maniola jurtina* (MASETTI & SCALI, 1976), but CARTER & WATT (1988) have shown that PGM heterozygosity of *Colias philodice eriphyle* varies with the date of sampling, which suggests a more complicated picture of adaptation of the different PGM alleles to temperature. The morphometric differentiation of the Morvan populations suggests selection pressure, phenotypic plasticity, or both.

Many questions may be raised at this stage in our study. In order to solve at least some of them we plan further work on *P. eunomia*, which will involve (1) pooling both electrophoresis and morphometric data by using the same or compatible methods of investigation in both French and Belgian laboratories ; (2) the collection of more specimens to allow detailed hierarchical analysis of both morphometric and biochemical characters ; (3) the study of further enzymes, in order to validate the estimation of genetic distances between populations and the use of Wright's *F* statistics ; (4) various DNA markers will also be tested, to complement the electrophoresis results ; (5) *P. eunomia* from other regions (e.g. Scandinavia, Bulgaria) will be studied, to investigate its global differentiation and its adaptations to various habitats ; it has been reported to feed on *Polygonum bistorta* in Belgium and France, on *Viola palustris* and possibly *Polygonum viviparum* in Scandinavia (HENRIKSEN & KREUTZER, 1982) and on *Vaccinium uliginosum* and *Andromeda polifolia* in Finland (MARTTILA *et al.* 1992).

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Variation saisonnière des peuplements de macrohétérocères en Navarre (Lepidoptera)

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Summary

The seasonal variation in the populations of macro-moths in Navarre, northern Spain, has been studied. The most common vegetational types were downy oak (*Quercus pubescens*), holm oak (*Q. ilex*) and Kermes oak (*Q. coccifera*) forests. The number and diversity of species increased between January and June, stabilising over the summer months, with a peak again in September, and dropped rapidly again from October. The larvae of species flying in winter and early spring generally feed on the leaves of trees, mainly beech, oak, pine and sallow. Such trees lose their importance as larval pabulum in moths flying later in the year; these tend to feed on annual plants. The best represented families were the Noctuidae and Geometridae.

Résumé

On a étudié la variation saisonnière des peuplements de macrohétérocères en Navarre (Nord de l'Espagne). Le nombre des espèces en vol et la diversité augmentent de janvier à juin, se stabilisent pendant l'été et subissent une forte baisse en octobre. Les espèces qui sont capturées en hiver et au début du printemps se nourrissent en général, à l'état larvaire, de feuilles d'arbre, surtout de fagacées, pinacées et de différentes salicacées. À mesure qu'avance le printemps, les arbres perdent de l'importance dans le régime alimentaire des chenilles, tandis que la consommation de plantes annuelles augmente. Les familles les plus riches en espèces sont les Noctuidae et Geometridae. Les formations végétales les plus fréquentes sont les rouvraies, les forêts de chêne vert (*Quercus ilex*) et les forêts de chêne kermès (*Q. coccifera*).

Resumen

Se estudia la variación estacional de las poblaciones de falenas en Navarra (Norte de España). El número de especies en vuelo y la diversidad va aumentando de enero a junio, se estabiliza en verano y en octubre sufre un brusco descenso. Las especies que vuelan en invierno y al comienzo de la primavera se alimentan en general, en estado larvario, de hojas de árboles, y a medida que avanza la primavera los árboles pierden importancia en el régimen alimentario de las orugas, mientras que aumenta el consumo de plantas anuales. Las familias más abundantes son Noctuidae y Geometridae. Las formaciones vegetales más ricas son quejigares, encinares y coscojares.

Introduction

Une des principales caractéristiques des écosystèmes méditerranéens est la différence thermique et pluviométrique importante qui existe entre les saisons, et même d'une année à l'autre. Cette «saisonnalité» marquée, ajoutée aux fluctuations interannuelles (en particulier en ce qui concerne la pluviométrie), donne lieu à une végétation très caractéristique, dont l'une des principales adaptations est la résistance à de longues périodes de sécheresse (CODY & MOONEY, 1978). Cependant, les adaptations morphologiques et physiologiques ne sont pas les seules stratégies que les plantes ont opposé aux irrégularités climatiques ; elles ont également développé des stratégies phénologiques grâce auxquelles les phénoménes vitaux fondamentaux (floraison, fructification, etc.) se sont ajustés avec précision aux conditions météorologiques. Bien évidemment, les plantes ne sont pas les seuls organismes qui subissent des fluctuations climatiques ; cependant, leur immobilité leur interdit les stratégies évasives comme les migrations, les diapauses, les comportements nocturnes, etc, que les animaux, et en particulier les insectes, peuvent mettre en pratique.

L'ajustement des cycles biologiques des insectes aux saisons est particulièrement marqué dans le cas des phytophages, qui doivent s'alimenter dans une période au cours de laquelle les plantes sont plus sensibles, à cause d'un faible taux en tanin ou bien de la présence d'organes adéquats pour l'alimentation des phytophages (feuilles, fleurs, fruits, etc.). Dans ce travail, nous analyserons les fluctuations de différentes variables écologiques des populations de macrohétérocères dans la province de Navarre (Nord de l'Espagne), tout au long de l'année, et en relation avec le type de végétation et l'utilisation du territoire. Concrètement, nous nous sommes interessés au nombre d'individus et d'espèces capturés chaque mois, à la diversité et à l'équitabilité, de même qu'à la variation de la composition des taxocénoses de ces lépidoptères.

Ce type d'étude dans la Péninsule Ibèrique n'a été antérieurement réalisé que par SARTO I MONTEYS (1984) dans le Massif du Montseny (Barcelone) et par YELA (1990) à Trillo (La Alcarria, Guadalajara).

Matériel et méthode

38 160 exemplaires de Lépidoptères adultes ont été capturés au moyen de pièges lumineux, pendant 15 ans, dans l'ensemble de la province de Navarre.

Les pièges étaient fixes, situés dans des centres agronomiques ou des fermes et ils fonctionnaient automatiquement de la tombée de la nuit jusqu'à l'aube. Au total, pour ce travail, les échantillons récoltés provenaient de 19 points

Tableau 1

Localités

UTM = Coordonnées selon un quadrillage de 10 km de côté. **Alt** = Altitude en mètres. **Vég.pot.** = Végétation potentielle, (R) représente forêt de rivière. **Usage** = On donne la principale utilisation du sol par rapport au nombre d'hectares total (que chacune occupe).

	UTM	Alt	Vég.pot.	Usage
1 Arizala	30TWN83	500	Chênaie vert	Culture non irriguée
2 Azcona	30TWM83	600	Chênaie vert	Culture non irriguée
3 Buñuel	30TXM24	200	Chênaie Kermès (R)	Culture irriguée
4 Cadreita	30TXM07	300	Chênaie Kermès (R)	Culture non irriguée
5 Carcastillo	30TXM29	300	Chênaie vert (R)	Culture irriguée
6 Cáseda	30TXN30	400	Chênaie vert (R)	Cult. irriguée et non irrig.
7 Fontellas	30TXM15	300	Chênaie Kermès (R)	Culture irriguée
8 Ilundáin	30TXN23	600	Rouvraie	Culture non irriguée
9 Imoz	30TWN95	600	Hêtraie	Feuillu
10 La Oliva	30TXM29	300	Chênaie vert	Culture non irriguée
11 Larraga	30TWN91	300	Chênaie vert (R)	Culture non irriguée
12 Lecároz	30TXN17	200	Chênaie	Feuillu
13 Marcilla	30TXM08	200	Chênaie Kermès	Cult. irriguée et non irrig.
14 Mendavia	30TWM69	300	Chênaie Kermès (R)	Culture non irriguée
15 Oteiza	30TWN81	500	Chênaie vert	Culture non irriguée
16 San Adrián	30TWM88	300	Chênaie Kermès (R)	Culture non irriguée
17 Sangüesa	30TXN41	400	Chênaie vert (R)	Culture non irriguée
18 Sartaguda	30TWM79	300	Chênaie Kermès (R)	Culture non irriguée
19 Ucar	30TXN02	500	Rouvraie	Culture non irriguée

de capture situés dans les formations végétales les plus communes de Navarre (Tableau 1).

La province de Navarre est située au nord de la Péninsule Ibérique, sa superficie est de 1 042 100 ha (10 421 km^2) et elle présente de forts gradients de direction nord-sud. Dans la partie septentrionale, le climat est nettement atlantique, avec des hivers doux et des étés frais et humides (Tableau 2) alors que dans la région centre et le sud de la province, les hivers sont froids et les étés chauds et secs. Le régime climatique induit une végétation très variée, comparable à celle de la région eurosibérienne dans le nord et à celle de la région méditerranéenne dans le sud. Ce gradient est accentué par la présence des Pyrénées à l'extrémité septentrionale et la vallée de l'Èbre dans la frange méridionale (Tableau 1).

Résultats

Au total, ont été capturés 38 160 exemplaires de papillons appartenant à 14 familles et 651 espèces, présentés en détail au Tableau 3.

On peut voir que la plupart des espèces appartiennent aux familles Noctuidae et Geometridae (81,9%) alors que la plupart des individus appartiennent aux familles Noctuidae et Arctiidae (respectivement 74 et 62%).

Tableau 2

Données climatiques

L = Latitude en degrés. **Années** = Période d'observation. **T** = Température moyenne en degré centigrade : **Ta** = Moyenne annuelle. **Tc** = Mois le plus chaud. **Tf** = Mois le plus froid. **TM** = Maxima des mois les plus froids. **TMC** = Maxima des mois les plus chauds. **Tm** = Minima des mois les plus froids. **P** = Précipitations en mm : **Pa** = Moyenne annuelle. **Pj** = Juin. **Pju** = Juillet. **Pa** = Août.

Localités	L	Années	Ta	Tc	Tf	TM	TMC	Tm	Pa	Pj	Pju	Pa
Arizala (1)	42	1960-80	13,1	22,3	5,8	9,7	29,2	2,0	703,7	66,1	31,8	26,3
Azcona (1)	42	1960-80	13,1	22,3	5,8	9,7	29,2	2,0	703,7	66,1	31,8	26,3
Buñuel	41	1932-80	14,0	23,6	5,7	9,3	30,7	2,1	413,6	41,9	20,2	26,4
Cadreita	42	1941-72	14,0	23,0	6,3	10,2	30,8	1,2	381,5	44,3	16,0	17,3
Carcastillo	42	1932-80	13,1	22,5	4,4	8,9	30,7	-0,1	473,2	43,5	20,5	29,9
Cáseda (2)	42	**	13,0	22,5	5,1	8,8	30,0	1,3	581,7	44,2	31,9	21,9
Fontellas (3)	42	1933-75	13,7	23,0	5,0	8,9	29,6	1,1	455,9	41,9	23,8	26,8
Ilundáin (4)	42	1931-80	12,2	20,3	4,8	8,6	26,9	1,0	999,3	74,6	45,4	43,5
Imoz (5)	42	1941-50	11,6	18,1	5,3	9,0	24,7	1,4	1260,3	47,1	43,9	54,8
La Oliva	42	1932-80	13,1	22,5	4,4	8,9	30,7	-0,1	473,2	43,5	20,5	29,9
Larraga (6)	42	1968-80	12,6	21,6	5,4	8,7	28,1	2,2	584,1	62,0	29,0	24,7
Lecároz (7)	43	1931-80	13,8	20,7	7,1	11,1	26,6	3,0	1792,3	95,2	74,0	89,7
Marcilla	42	1950-79	13,8	22,7	5,5	9,7	29,8	1,4	451,7	44,1	23,9	22,2
Mendavia (8)	42	***	13,3	22,1	5,3	9,0	29,1	1,6	337,2	50,1	14,3	21,4
Oteiza (6)	42	1968-80	12,6	21,6	5,4	8,7	28,1	2,2	584,1	62,0	29,0	24,7
San Adrián (9)	42	1931-80	13,3	22,1	5,3	9,0	29,1	1,6	495,5	50,8	33,0	28,1
Sangüesa (2)	42	**	13,0	22,5	5,1	8,8	30,0	1,3	581,7	44,2	31,9	21,9
Sartaguda	42	1931-80	13,3	22,1	5,3	9,0	29,1	1,6	495,5	50,8	33,0	28,1
Ucar (6)	42	1968-80	12,6	21,6	5,4	8,7	28,1	2,2	584,1	62,0	29,0	24,7

(1) Les données correspondent à Alloz. (2) Données de température de Janvier (** années 1955-1980) et précipitations de Sangüesa (** années 1911-1936). (3) Données de Tudela. (4) Données de Pamplona. (5) Données de Lecumberri. (6) Données de Mendigorría. (7) Données de Santesteban. (8) Données de température de Sartaguda (*** années 1931-1980) et précipitations de Mendavia-Imoz (*** années 1967-1975). (9) Données de Sartaguda.

Pour pouvoir comparer les échantillons, nous n'avons pas retenu les localités présentant des données fragmentaires ou incomplètes. Dix-neuf localités présentaient un échantillon à peu près homogène et ont donc été conservées. Groupées par mois, les 20 espèces les plus abondantes sont présentées aux Tableaux 4.1 à 4.12. On peut noter qu'en janvier et février (Tableaux 4.1 et 4.2) il y a peu d'espèces et d'individus en vol, bien qu'une légère augmentation apparaisse. Les espèces les plus abondantes sont les mêmes pour ces deux mois, une noctuelle et une géomètre. Si l'on prend en compte l'alimentation larvaire de ces espèces (selon les données de Gomez De Aizpurua, 1985 ; 1987a ; 1987b ; 1988 ; Soria Carreras, 1987 ; Templado, 1990) en général, leurs plantes nourricières sont, par ordre d'importance, les fagacées (*Quercus* et *Castanea*), les pinacées (*Pinus*), cistacées, salicacées et rosacées, essentiellement donc des arbres et arbustes ; les plantes herbacées n'interviennent pratiquement pas. Bien évidement, ces espèces hibernent en phase adulte princi-

Tableau 3

Nombre d'individus capturés chaque mois et par familles

	J	F	M	A	M	J	J	A	S	O	N	D	Total	N° esp.
Hepialidae	-	-	-	-	-	-	2	13	19	13	1	-	47	1
Cossidae	-	-	-	33	35	166	260	45	3	-	-	-	542	5
Saturniidae	-	-	1	16	32	9	1	-	-	-	-	-	59	4
Lasiocampidae	-	1	22	13	9	255	574	244	350	61	9	9	1547	19
Sphingidae	-	-	-	19	152	348	166	208	86	6	2	-	987	14
Drepanidae	-	-	-	-	4	6	2	26	27	1	1	-	67	4
Axiidae	-	-	-	-	-	1	-	-	-	-	-	-	1	1
Thyatiridae	-	-	-	17	19	7	5	4	3	1	-	-	56	6
Geometridae	14	25	121	199	275	520	839	926	815	377	207	29	4347	200
Thaumetopoeidae	-	-	-	-	-	5	191	554	119	-	-	-	869	2
Notodontidae	-	1	29	208	128	78	59	36	21	1	4	3	568	21
Lymantriidae	-	-	-	-	4	35	333	172	49	2	-	-	595	9
Arctiidae	1	3	4	290	761	1320	1633	2193	1948	333	7	-	8493	32
Noctuidae	190	195	517	565	1004	2011	2957	3081	3375	3527	2277	282	19982	333
Total :	205	225	694	1360	2423	4761	7022	7502	6814	4322	2508	323	38160	651

Tableaux 4.1-4.12

Nombre d'individus capturés par mois

Chênaie = **1** : Lecároz. **Hêtraie** = **2** : Imoz. **Rouvraie** = **3** : Ilundáin 1983. **4** : Ilundáin 1984. **5** : Ucar. **Forêt de chêne vert** = **6** : Arizala. **7** : Azcona. **8** : Oteiza. **9** : Larraga. **10** : Sangüesa. **11** : Cáseda. **12** :Carcastillo. **13** : La Oliva. **Forêt de chêne Kermès** = **14** : Mendavia. **15** : Sartaguda1984. **16** : Sartaguda1985. **17** :San Adrián. **18** : Marcilla. **19** : Cadreita. **20** : Fontellas. **21** : Buñuel.

h (hibernation) : o = œuf, ch = chenille, c = chrysalide, i = imago.

Tableau 4.1 : Janvier

Localités :	9	13	18	h
Conistra alicia	-	5	17	i
Chemerina caliginearia	3	1	2	c,i
Agrochola lychnidis	1	2	-	o
Agrochola lota	-	-	2	i
Peridroma saucia	-	2	-	ch,c
Colotois pennaria	-	-	1	o
N° exemplaires :	4	10	22	
N° espèces :	2	4	4	

Tableau 4.2 : Février

Localités :	9	13	18	h
Conistra alicia	5	22	15	i
Chemerina caliginearia	3	2	2	c,i
Xylena exsoleta	-	3	-	i
Conistra torrida	2	-	-	i
Chesias rufata	-	-	1	c
Orthosia incerta	-	-	1	c
Orthosia stabilis	-	-	1	c
Pyrois cinnamomea	-	1	-	i
N° exemplaires :	10	28	20	
N° espèces :	3	4	5	

Tableau 4.3 : Mars

Localités :	9	11	13	14	18	h
Orthosia incerta	3	78	14	2	17	c
Conistra alicia	2	41	4	4	8	i
Orthosia gothica	6	18	12	-	11	c
Valeria jaspidea	-	26	6	-	2	c
Chemerina caliginearia	7	5	3	5	3	c,i
Cerastis rubricosa	3	14	2	1	-	c
Trichiura ilicis	8	2	1	1	-	ch
Biston strataria	-	3	-	-	7	c
Xylocampa areola	1	5	1	-	3	c
Chesias rufata	1	7	-	1	-	c
Orthosia stabilis	1	5	-	-	2	c
Spudaea ruticilla	1	6	-	1	-	c,i
Alsophila aescularia	-	6	-	1	-	c
Xylena exsoleta	1	4	1	-	1	i
Orthosia gracilis	-	3	2	-	1	c
Cerura iberica	-	-	2	1	1	c
N° exemplaires :	37	240	52	26	60	
N° espèces :	13	27	15	16	15	

Tableau 4.4 : Avril

Localités :	3	4	5	6	9	11	13	15	16	17	18	20	h
Diaphora mendica	-	3	22	15	8	1	44	-	-	-	1	5	ch
Phragmatobia fuliginosa	-	2	9	-	1	6	6	-	11	-	15	8	ch
Orthosia gracilis	-	1	-	-	1	12	-	-	-	-	15	1	c
Mythimna sicula	-	4	6	9	7	10	-	-	-	-	-	-	ch
Parahypopta caestrum	-	-	-	-	-	-	-	-	-	32	-	-	ch
Valeria jaspidea	-	-	5	1	1	6	-	-	-	-	7	-	c
Orthosia gothica	-	-	1	1	2	9	-	-	-	-	8	-	c
Cerura iberica	-	-	1	3	-	5	8	-	1	-	4	-	c
Egira conspicillaris	-	7	2	3	-	7	1	-	-	-	-	1	c
Pheosia tremula	-	1	-	2	2	2	3	2	-	-	8	-	c
Orthosia incerta	-	-	-	-	3	11	-	-	-	-	3	-	c
Autographa gamma	-	1	5	8	1	-	1	-	-	-	1	-	ch
Orthosia miniosa	-	-	-	-	3	9	2	-	-	-	-	-	c
Cerastis rubricosa	-	1	7	1	-	1	2	-	-	-	1	-	c
Chesias rufata	-	-	2	-	2	3	3	-	-	-	2	-	c
Pterostoma palpina	-	-	1	-	1	2	2	-	-	-	6	-	c
Aleucis distinctata	-	2	5	-	1	4	-	-	-	-	-	-	c
Clostera pigra	-	-	-	-	-	-	5	-	1	-	5	-	c
Ocnogyna zoraida	-	-	-	-	-	8	3	-	-	-	-	-	c
Clostera curtula	-	-	-	2	-	3	1	1	-	-	2	-	c
N° exemplaires :	6	47	85	61	47	129	109	7	30	33	110	39	
N° espèces :	5	23	26	23	21	36	34	5	18	2	36	20	

Tableau 4.5 : Mai

Localités :	1	3	4	5	6	9	11	12	13	17	18	21	h
Mythimna vitellina	-	7	-	10	15	-	5	116	2	-	29	3	ch
Diaphora mendica	-	3	-	34	5	10	18	1	70	-	1	22	ch
Phragmatobia fuliginosa	1	1	-	2	13	-	2	-	31	12	31	11	ch
Spilosoma lubricipeda	3	-	-	-	-	3	2	3	31	8	24	3	c
Mythimna sicula	-	2	-	11	-	6	25	4	4	2	6	1	ch
Laothoe populi	-	1	-	1	1	-	15	-	4	1	11	-	c
Ochropleura plecta	6	-	-	-	-	-	1	-	13	3	9	2	c
Aspitates ochrearia	-	-	2	5	-	1	2	1	4	3	11	4	ch
Dyspessa ulula	-	-	-	2	11	1	-	11	3	1	1	-	ch
Mythimna albipuncta	-	-	-	-	3	-	8	4	2	-	10	-	ch
Idaea subsericeata	-	-	1	5	-	1	4	1	2	2	6	1	ch
Cerura iberica	-	-	-	1	1	1	7	-	2	-	8	1	c
Deilephila porcellus	-	-	-	-	-	-	19	1	-	-	-	-	c
Tephrina murinaria	-	-	-	1	1	3	2	-	1	1	10	-	?
Noctua pronuba	-	2	-	2	2	-	-	8	2	-	3	-	ch
Smerinthus ocellata	-	-	-	-	-	-	12	-	2	-	3	-	c
Hoplodrina ambigua	-	-	-	3	1	1	-	5	1	-	4	2	ch
Hadena perplexa	-	-	-	-	-	3	3	4	3	-	3	1	c
Xestia c -nigrum	2	-	-	-	1	-	1	-	4	-	9	-	ch
Phlogophora meticulosa	-	-	-	2	-	-	-	1	2	-	6	5	o,ch,c,i
N° exemplaires :	24	21	18	129	82	50	186	181	215	44	270	94	
N° espèces :	14	11	15	42	25	27	50	31	41	14	60	38	

Tableau 4.6 : Juin

Localités :	1	2	3	4	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Phragmatobia fuliginosa	1	-	4	2	2	1	-	9	12	4	-	91	30	25	22	37	115	-	13
Mythimna vitellina	2	5	17	2	4	47	4	-	5	21	26	12	8	5	2	4	48	-	3
Eilema caniola	3	-	23	6	1	16	-	-	32	60	5	1	13	1	6	4	8	-	-
Spilosoma lubricipeda	4	-	-	-	-	-	-	1	-	1	1	25	37	2	9	58	19	-	4
Deilephila porcellus	-	-	-	2	-	-	-	11	11	63	-	27	1	-	-	3	1	-	-
Synthymia fixa	-	-	2	1	1	52	2	2	-	46	-	-	-	-	7	-	-	-	-
Hoplodrina ambigua	4	-	25	2	-	11	-	5	3	17	2	8	8	-	3	1	12	1	4
Dyspessa ulula	-	-	-	-	50	6	-	3	6	6	18	3	3	-	1	5	-	-	-
Lacanobia oleracea	1	-	-	-	1	2	-	1	12	4	-	25	11	2	1	11	24	-	4
Malacosoma castrensis	-	-	-	-	-	22	10	26	18	8	-	6	1	-	1	-	1	-	-
Emmelia trabealis	-	-	2	3	-	40	-	1	24	4	-	1	5	2	2	2	5	-	1
Arctia villica	-	-	-	-	13	12	5	8	1	5	1	2	9	-	5	4	10	-	10
Laothoe populi	-	-	-	-	-	-	-	3	-	24	-	10	13	-	2	1	17	-	-
Agrotis exclamationis	1	1	1	2	4	17	4	4	1	4	2	3	23	-	1	-	2	-	-
Acontia lucida	-	-	1	4	-	-	-	-	22	-	-	-	3	2	-	8	10	-	2
Tyta luctuosa	-	-	3	8	-	4	-	-	11	2	2	2	2	1	4	1	6	-	1
Semiothisa clathrata	-	-	7	13	-	1	-	1	5	3	-	-	6	3	5	-	-	-	3
Malacosoma neustria	-	-	1	-	-	5	1	11	9	1	-	10	-	-	3	-	3	-	-
Oria musculosa	-	-	2	-	-	2	4	21	-	4	-	-	5	-	3	-	2	-	-
Scopula incanata	-	-	19	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N° exemplaires :	51	13	225	163	123	349	47	151	227	461	70	296	333	63	108	157	422	1	69
N° espèces :	27	8	56	53	25	63	19	37	45	78	14	51	83	27	41	24	71	1	29

Tableau 4.7 : Juillet

Localités :	1	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Phragmatobia fuliginosa	-	1	34	12	4	-	2	43	13	1	17	157	105	8	13	125	64	5	-	36
Emmelia trabealis	-	26	59	39	9	-	153	1	10	-	8	16	19	11	14	9	-	8	1	53
Eremobia ochroleuca	-	2	57	102	51	-	171	10	2	-	2	10	4	-	-	-	-	-	-	-
Malacosoma castrensis	1	4	34	44	49	-	158	19	10	-	12	8	2	-	-	1	2	-	-	-
Lymantria dispar	-	-	8	10	1	-	22	12	29	-	35	33	12	-	1	63	4	-	-	5
Tyta luctuosa	-	6	63	18	7	-	34	2	5	-	8	10	13	1	4	10	3	14	-	19
Eilema caniola	-	13	80	15	9	-	5	-	14	-	32	2	25	13	2	5	1	1	-	-
Eilema complana	-	37	167	4	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Thaumetopoea pityocampa	-	2	80	13	2	-	-	5	7	-	-	22	7	-	-	14	3	-	10	9
Acontia lucida	-	1	43	3	1	-	-	-	7	-	2	13	14	4	1	28	2	15	-	30
Oria musculosa	-	1	25	7	26	-	40	1	2	-	28	-	-	2	-	3	-	-	-	-
Chelis maculosa	-	-	72	30	29	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Parahypopta caestrum	-	-	-	5	-	-	7	5	-	1	6	3	79	2	4	1	3	1	-	8
Idaea ochrata	-	10	25	49	5	-	23	-	2	-	2	-	2	-	1	-	1	-	-	1
Malacosoma neustria	-	4	19	9	11	-	36	2	2	1	7	2	1	2	-	1	1	-	-	-
Euproctis chrysorrhoea	-	-	-	60	6	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
Synthymia fixa	-	13	32	7	8	-	2	1	-	1	-	1	-	-	-	-	-	-	-	-
Tephrina murinaria	-	-	3	5	-	-	12	9	4	-	1	4	10	3	4	2	3	1	-	4
Semiothisa clathrata	-	-	25	1	-	-	2	-	-	-	-	6	13	1	-	-	1	1	-	12
Heliothis viriplaca	-	-	13	-	1	-	-	7	-	-	-	19	5	-	-	2	2	3	-	-
N° exemplaires :	4	177	1404	580	288	1	767	156	134	33	213	391	506	73	74	370	124	86	19	405
N° espèces :	4	42	136	73	54	1	56	38	26	13	33	55	84	26	31	58	33	29	8	63

Tableau 4.8 : Août

Localités :	1	2	3	4	5	6	7	8	9	10	11	13	14	15	16	17	18	19	21
Eilema complana	-	-	208	293	2	10	-	-	-	3	-	-	3	-	-	-	-	-	-
Eilema pygmaeola	3	-	220	268	-	2	-	1	-	1	-	-	-	1	-	-	-	-	-
Emmelia trabealis	-	-	72	75	-	14	-	56	-	24	-	19	21	77	1	-	18	14	80
Phragmatobia fuliginosa	7	9	7	118	-	-	-	-	2	14	1	82	26	42	7	7	31	35	29
Tyta luctuosa	-	2	35	103	-	26	-	19	1	14	-	5	22	29	-	-	13	15	25
Thaumetopoea pityocampa	2	2	7	125	-	6	-	5	5	3	-	18	24	6	2	1	8	21	22
Eilema caniola	2	-	32	103	-	1	-	-	-	6	2	6	1	5	1	-	5	-	3
Acontia lucida	-	1	4	31	-	-	-	-	-	13	-	1	10	16	-	-	4	25	44
Tephrina murinaria	-	-	2	2	-	-	-	13	54	2	1	8	23	4	8	-	1	19	8
Lymantria dispar	2	-	1	10	-	-	-	4	-	89	-	1	17	5	1	-	-	1	10
Abraxas pantaria	-	-	-	-	-	-	-	-	-	-	-	-	1	64	22	7	-	6	-
Autographa gamma	5	6	10	37	-	-	-	-	3	-	-	5	3	4	-	-	4	5	4
Heliothis viriplaca	-	2	2	41	-	1	-	-	4	-	-	7	6	1	-	-	2	1	10
Rhodometra sacraria	2	7	27	8	-	1	-	-	-	-	-	-	-	15	-	-	-	1	3
Arctia caja	-	3	-	26	-	4	-	-	-	-	1	14	2	-	-	2	7	-	-
Noctua janthina	-	1	3	46	-	-	-	-	-	-	-	4	-	1	-	-	-	2	1
Agrotis crassa	-	48	-	5	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Smerinthus ocellata	1	1	-	-	-	-	-	-	1	-	23	6	9	-	-	1	13	-	-
Laothoe populi	1	1	-	2	-	2	-	-	3	-	6	17	4	1	-	4	9	-	1
Malacosoma neustria	-	46	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
N° exemplaires :	103	199	795	1842	4	93	1	167	119	202	48	280	266	362	72	39	193	199	409
N° espèces :	46	44	61	138	3	23	1	25	29	30	16	46	51	53	24	17	47	45	61

Tableau 4.9 : Septembre

Localités :	2	3	4	5	6	8	9	11	13	14	15	16	17	18	19	21
Phragmatobia fuliginosa	1	25	32	16	5	2	3	1	97	68	138	3	9	28	13	29
Eilema caniola	1	163	111	67	7	3	-	-	5	14	19	1	3	7	1	11
Cymbalophora pudica	-	58	55	24	7	24	47	-	60	1	5	2	14	25	15	15
Abraxas pantaria	-	-	-	1	-	-	-	-	-	4	219	-	-	-	63	-
Emmelia trabealis	-	14	36	109	-	83	-	-	-	5	29	-	-	1	-	7
Hoplodrina ambigua	2	73	89	26	1	4	-	-	3	2	19	-	25	2	4	22
Xestia xanthographa	7	61	106	17	1	4	5	-	10	-	-	1	10	29	1	3
Tyta luctuosa	-	9	81	61	3	59	-	-	-	7	19	1	-	2	-	2
Lasiocampa trifolii	-	13	16	42	73	38	13	1	10	1	-	1	1	10	-	3
Eilema complana	-	1	157	13	5	-	-	-	-	-	-	-	-	-	-	-
Mythimna vitellina	8	34	15	31	22	19	14	1	8	1	1	-	2	10	-	6
Noctua pronuba	20	55	36	10	12	7	-	-	1	-	1	-	1	4	1	-
Luperina testacea	9	13	28	6	5	3	4	-	19	-	-	1	17	14	4	1
Thaumetopoea pityocampa	1	-	39	43	10	3	-	-	1	13	2	-	-	-	-	2
Acontia lucida	-	17	15	23	-	4	-	-	-	6	39	-	-	2	1	2
Thalpophila vitalba	1	25	28	10	4	1	4	-	2	1	-	1	3	1	1	-
Rhodometra sacraria	2	31	8	4	-	1	1	-	-	-	14	-	5	-	1	2
Athetis hospes	-	2	1	1	-	-	1	-	-	-	24	-	2	1	9	21
Noctua janthina	4	7	34	4	1	4	1	-	3	-	2	-	1	-	-	-
Arctia caja	-	1	12	2	15	1	-	1	2	14	-	-	-	4	-	1
N° exemplaires :	118	815	1300	658	244	346	172	11	276	236	666	20	143	222	149	223
N° espèces :	30	97	132	91	47	53	42	8	31	45	65	16	45	52	31	52

Tableau 4.10 : Octobre

Localités :	1	3	4	5	6	8	9	11	13	14	15	16	17	18	19	20
Omphaloscelis lunosa	3	16	25	21	-	1	27	21	32	19	2	-	11	54	21	2
Agrochola lychnidis	-	11	29	3	1	-	15	27	18	2	-	1	2	45	67	1
Xestia xanthographa	2	5	16	15	-	-	9	6	21	19	1	-	6	100	22	-
Eilema caniola	-	5	8	76	-	1	1	1	-	21	51	1	-	2	9	-
Luperina testacea	-	1	16	3	1	-	1	2	22	55	3	-	2	12	4	-
Hoplodrina ambigua	-	2	20	7	1	-	1	2	-	20	15	-	6	11	20	-
Aporophila nigra	-	5	12	19	-	1	-	8	10	4	2	3	4	28	3	-
Xanthia ocellaris	-	-	1	2	-	-	2	6	22	4	-	-	3	54	1	-
Trigonophora jodea	-	6	6	4	-	2	15	22	13	2	-	-	3	12	7	-
Paradiarsia glareosa	-	11	13	8	-	1	28	13	11	3	-	-	-	2	1	-
Noctua pronuba	2	5	9	13	3	-	9	6	2	4	7	-	2	12	12	4
Aporophyla lutulenta	-	7	7	10	-	-	29	12	8	1	-	-	-	8	-	-
Cladocerotis optabilis	-	-	1	9	3	1	17	10	13	-	-	1	1	9	2	1
Enconista miniosaria	-	11	1	16	-	1	9	1	7	-	-	1	-	13	1	-
Trigonophora flammea	-	5	7	13	1	-	7	2	10	1	-	-	5	8	2	-
Mythimna unipuncta	7	1	-	1	-	-	-	5	2	-	-	-	-	34	6	-
Phlogophora meticulosa	1	2	3	-	2	-	3	5	9	5	2	-	-	15	4	-
Rhodometra sacraria	1	4	1	7	-	-	-	4	-	1	12	-	1	12	-	-
Mythimna albipuncta	-	-	3	3	-	-	-	14	2	3	2	-	-	11	3	-
Cymbalophora pudica	-	-	-	-	-	-	4	-	3	9	6	4	3	5	6	-
N° exemplaires :	25	152	249	313	18	13	239	286	301	263	147	24	89	611	299	10
N° espèces :	10	17	58	51	12	10	44	63	51	57	39	15	29	76	59	6

Tableau 4.11 : Novembre

Localités :	1	3	4	5	6	8	9	11	13	15	16	18	19	20	21	h
Agrochola lychnidis	-	28	12	96	5	17	119	102	76	26	26	113	104	15	49	o
Mythimna unipuncta	12	-	-	-	-	-	1	1	-	10	-	6	43	4	56	ch
Xestia c -nigrum	1	-	1	-	-	-	-	3	-	7	1	1	18	1	48	ch
Omphaloscelis lunosa	-	-	-	3	-	1	10	2	5	1	-	32	2	4	20	ch
Conistra alicia	-	-	-	-	-	-	3	37	8	-	-	26	4	-	-	i
Noctua pronuba	-	-	1	-	-	-	2	-	3	7	1	8	2	21	20	ch
Aporophila nigra	-	2	5	1	1	1	2	2	-	12	3	7	3	5	17	ch
Rhizedra lutosa	-	-	-	1	-	-	2	8	4	-	-	10	-	-	27	o
Agrochola lota	-	-	-	-	-	-	-	34	6	-	-	4	3	-	-	i
Larentia clavaria	-	-	-	-	-	-	-	-	2	-	1	23	12	1	-	o
Hoplodrina ambigua	-	-	1	1	-	1	1	-	-	7	-	-	8	-	19	ch
Agrochola helvola	-	4	2	1	-	1	3	23	1	-	-	1	-	-	-	o
Trigonophora jodea	-	-	4	2	-	-	6	2	4	-	1	7	3	1	6	?
Xanthia ocellaris	-	-	-	1	-	-	-	-	-	-	1	10	10	2	8	o
Xanthia gilvago	-	-	-	-	-	-	1	3	-	1	1	2	3	10	8	o
Rhodometra sacraria	-	5	-	-	-	-	1	-	-	10	1	1	2	2	7	ch,i
Phlogophora meticulosa	1	-	1	-	-	-	2	1	1	-	-	9	2	2	9	o,ch,c,i
Mythimna loreyi	-	1	-	-	-	-	1	3	-	-	3	1	3	2	12	ch
Enconista miniosaria	-	3	6	3	-	-	4	1	1	2	-	2	1	-	2	o
Colotois pennaria	-	12	-	-	-	1	-	1	6	-	-	2	1	1	-	o
N° exemplaires :	34	89	74	134	6	30	177	265	126	114	52	278	255	83	358	
N° espèces :	12	24	34	24	2	10	27	30	19	28	16	30	28	21	32	

Tableau 4.12 : Décembre

Localités :	3	4	6	11	15	16	18	19	h
Agrochola lychnidis	9	1	25	-	20	1	1	4	o
Mythimna unipuncta	1	-	-	-	4	-	-	21	ch
Conistra alicia	-	-	-	19	-	-	2	4	i
Agrochola lota	-	1	-	8	4	2	-	3	i
Agrotis ipsilon	2	-	-	-	-	-	-	7	o,ch,c,i
Conistra daubei	7	2	-	-	-	-	-	-	i
Peridroma saucia	3	-	-	-	1	-	-	5	ch,c
Agrochola blidaensis	3	3	-	-	-	-	-	-	?
Colotois pennaria	3	-	2	-	-	-	-	-	o
Aporophila nigra	-	1	-	-	3	-	-	-	ch
N° exemplaires :	39	13	28	30	46	7	6	50	
N° espèces :	16	9	3	4	14	5	4	11	

palement, bien que quelques-unes le fassent en phase chrysalide ou même chenille, ce qui indiquerait que les adultes de janvier et février seraient le produit d'une émergence précoce. Dans le cas de *Agrochola lychnidis* et *Colotois pennaria*, il s'agit d'espèces qui hibernent sous forme d'œuf ; janvier et février correspondent alors à la fin de leur période de vol. Notons de plus, que les localités où ont été capturés les individus de ces espèces se trouvent toutes dans le sud de la province : Larraga (9), La Oliva (13) et Marcilla (18), là où la végétation potentielle se compose de *Quercus ilex* (chêne vert, les deux premières) et *Quercus coccifera* (chêne Kermès, la dernière).

En mars, on note une augmentation sensible du nombre d'exemplaires et d'espèces (Tableau 4.3). On trouve en particulier *Conistra alicia* et *Chemerina caliginearia*, mais également quelques *Orthosia* sont déjà plus abondantes (*O. incerta* et *O. gothica*). L'alimentation larvaire des imagos capturés en mars se réalise surtout au dépend des arbres (*Quercus*, *Fagus*, *Salix*, *Populus*, *Ulmus*, *Tilia*, *Betula*, etc.) ou arbustes (*Crataegus*, *Malus*, *Prunus*, *Genista*, etc.). Les espèces les plus abondantes sont en général celles qui passent l'hiver au stade chrysalide.

En avril, le nombre d'individus et d'espèces en vol continue à augmenter (Tableau 4.4). Onze des seize espèces de mars se capturent encore, auxquelles s'ajoutent six nouvelles. Bien que deux Arctiides soient en tête de la liste d'abondance (*Diaphora mendica* et *Phragmatobia fuliginosa*), les plus abondants sont les Noctuides ; les Géométrides sont encore rares. Les zones comptant le plus d'individus et d'espèces capturés sont la région moyenne et la Ribera (centre et sud de la Navarre), bien qu'apparaissent déjà des individus dans la région nord. L'alimentation larvaire des imagos capturés en avril, se réalise principalement sur des plantes basses annuelles, tant sylvestres que cultivées, bien que les premières soient les plus importantes. L'abondance de celles qui s'alimentent sur les arbres ou arbustes à feuilles caduques (fagacées et salicacées) diminue. Les espèces les plus abondantes ont hiberné au stade chenille, probablement non complètement développées.

En mai, la tendance à l'augmentation s'accentue (Tableau 4.5). Les localités de la vallée de l'Èbre et de la zone moyenne sont toujours les plus riches. En effet, en mai, des gelées peuvent toujours se produire dans la région nord, et les températures moyennes nocturnes sont encore basses en montagne. Les espèces les plus abondantes sont les Noctuides (*Mythimna vitellina*) et les Arctiides (*Diaphora mendica* et *Phragmatobia fuliginosa*), bien qu'apparaissent déjà des Sphyngides, Géométrides et Cossides. L'alimentation larvaire des espèces les plus abondantes repose surtout sur les plantes basses de la famille des Astéracées et des Poacées.

En juin, on peut noter une grande augmentation du nombre d'individus et d'espèces en vol, même dans le nord de la province (Tableau 4.6). Parmi les 10 espèces les plus abondantes, on trouve trois Arctiides (*P. fuliginosa*, *Eilema caniola* et *Spilosoma lubricipeda*) et quatre Noctuides, bien que la densité de celles-ci commence à diminuer à partir de ce mois. L'alimentation larvaire des espèces les plus abondantes se réalise sur les Astéracées et dans une moindre mesure les Poacées et Fabacées.

En juillet, les captures du nord de la province prennent de l'importance tandis que celles du sud commencent à se raréfier (Tableau 4.7). De nouveau, l'espèce la plus abondante est l'Arctiide (*P. fuliginosa*). Les Noctuides les plus abondantes sont *Emmelia trabealis*, *Tyta luctuosa* et *Acontia lucida*. Les espèces *Malacosoma castrensis*, *Lymantria dispar* et *Thaumetopoea pityocampa* sont également représentées. Les larves des espèces les plus abondantes s'alimentent de la strate herbacée (Astéracées, Poacées, Polygonacées, Plantaginacées, etc.) et quelques-unes également exploitent la strate arborée (Fagacées et Pinacées), en particulier dans la région nord de la province.

En août, les captures sont toujours très abondantes, bien que les localités du sud y contribuent de moins en moins (Tableau 4.8). En général, les Arctiides sont toujours les plus abondants ; les Noctuides les plus communes sont, comme le mois précédent *Emmelia trabealis*, *Tyta luctuosa* et *Acontia lucida*. Les espèces les plus abondantes continuent à exploiter en priorité la strate herbacée ainsi que les lichens, ceci étant dû sans doute à la présence des deux espèces d'*Eilema*.

En septembre, les captures sont toujours abondantes au nord de la province et elles reprennent de l'importance dans le sud (Tableau 4.9). Les Arctiides déjà citées sont toujours en tête de la liste de captures. Viennent s'y ajouter les Lasiocampides (*Lasiocampa trifolii*) ou Géométrides (*Abraxas pantaria*) et surtout les noctuides (*Emmelia trabealis*, *Hoplodrina ambigua*, *Xestia xanthographa*, *Tyta luctuosa*, *Mythimna vitellina* et *Noctua pronuba*). Les plantes nourricières des larves sont encore les Astéracées, Poacées et Polygonacées et les Rosacées prennent de l'importance.

En octobre, on note une forte baisse, tant du nombre d'individus capturés que du nombre d'espèces (Tableau 4.10). Parmi les dix espèces les plus abondantes, neuf sont des Noctuides et la dixième une Arctiide. Les localités qui comptent le plus grand nombre d'individus capturés sont situées dans la région moyenne et la Ribera. L'alimentation des larves se fait aux dépens des plantes herbacées annuelles comme les Poacées, Astéracées, Fabacées et Polygonacées. En parallèle, commencent à apparaître des adultes dont les larves se nourrissent de Rosacées et de Salicacées.

En novembre, la baisse du nombre d'individus et d'espèces capturés, en particulier dans le nord de la province, s'accentue (Tableau 4.11). Les espèces les plus communes appartiennent à la famille des Noctuides (*Agrochola lychnidis*, *Mythimna unipuncta*, etc.). L'alimentation larvaire des espèces les plus abondantes se réalise sur les Rosacées, Poacées, Salicacées et Fabacées, avec une exploitation encore plus importante des plantes basses annuelles que des arbres ou arbustes. Les espèces capturées en novembre hibernent en général au stade œuf bien que quelques-unes le fassent au stade chenille.

En décembre, on note une forte diminution des captures (Tableau 4.12). Parmi les dix espèces les plus abondantes, il y a neuf Noctuides et une Géométride. Les plantes exploitées par les larves sont les mêmes qu'au cours du mois précédent. Les espèces capturées en décembre hibernent à différents stades, mais on note que les espèces qui hibernent au stade imago prennent de l'importance.

En résumé, et si l'on considère les dix espèces les plus abondantes, chaque mois (numerotées de 1 à 10) en fonction du nombre d'individus capturés (Tableau 5), on peut noter que peu d'espèces sont représentées dans ce tableau car pour la plupart, elles sont présentes pendant plusieurs mois.

On trouve deux Cossidae, trois Lasiocampidae, deux Sphingidae, huit Geometridae (deux Larentiinae et six Boarmiinae), une Thaumetopoeidae, deux Notodontidae, une Lymantriidae, sept Arctiidae et quarante Noctuidae (une Catocalinae, deux Acontiinae, six Amphipyrinae, treize Cuculliinae, dix Hadeninae et huit Noctuinae). Les Arctiides prédominent sur le reste, grâce surtout à l'abondance de *Phragmatobia fuliginosa* au printemps et en été. Les Noctuides dominent en automne et en hiver, bien qu'elles soient abondantes toute l'année.

Discussion

Les espèces qui sont capturées en hiver et au début du printemps (de décembre à mars) se nourrissent en général, à l'état larvaire, de feuilles d'arbre, surtout de Fagacées (*Quercus*, *Castanea*, etc.), Pinacées (*Pinus*) et de différentes Salicacées. À mesure qu'avance le printemps, les arbres perdent de l'importance dans le régime alimentaire des chenilles, tandis que la consommation de plantes annuelles augmente (Astéracées et Poacées principalement).

Si l'on observe les cycles biologiques de ces espèces hibernantes, il apparaît que la phase chenille est atteinte au printemps et que ces animaux passent la période été-hiver au stade chrysalide ou parfois imago.

Dans tous les cas, les chenilles utilisent les feuilles des arbres au moment le plus approprié pour l'alimentation. En effet, il a été démontré que le contenu en tanin des feuilles augmente et qu'elles perdent de l'eau à mesure qu'avance le printemps (SCRIBER & SLANSKY, 1981) et en réponse aux premières attaques des herbivores, de sorte que leur qualité nutritive diminue. Une telle relation a été décrite pour le chêne et *Operophtera brumata* L. (Geometridae) (FEENY, 1970), et *Lymantria dispar* L. (Lymantriidae) (SCHULTZ & BALDWIN, 1982), et enfin pour différents lépidoptères mineurs (FAETH *et al.*, 1981 ; FAETH, 1986 ; 1988). Ce renforcement des défenses chimiques des arbres peut même être induit à distance comme le suggèrent BALDWIN & SCHULTZ (1983) pour les peupliers et les érables.

L'utilisation par les chenilles des feuilles des arbres au printemps n'est pas une exclusivité, parmi les lépidoptères, des hétérocères ; en effet, il est bien connu que les Lycénides, qui hibernent au stade œuf, se nourrissent de feuilles d'arbres au cours des premiers mois du printemps (MARTIN CANO, 1982). Les plantes ont développé divers mécanismes pour prévenir les attaques des phytophages et ceux-ci, de leur côté, ont essayé d'esquiver ou éviter ces mécanismes (RHOADES, 1985). Le résultat de cette interaction est en définitive un ajustement chaque fois plus fin entre l'hôte et l'herbivore. Cet ajustement se manifeste non seulement au niveau physiologique (présence de tanins, toxines, etc.), mais aussi au niveau de la synchronisation des cycles vitaux de la plante et de l'insecte phytophage (STRONG *et al.*, 1984 ; TEMPLADO, 1990). Ce dernier aspect est une fois encore mis en évidence par nos résultats.

Les espèces qui volent dès le mois d'avril se trouvent à l'état larvaire de mai à novembre avec estivation et hibernation à différents stades. Leur alimentation larvaire est principalement constituée de plantes herbacées annuelles, chez lesquelles la défense chimique contre les herbivores ne se base pas tant sur la présence de tanins que sur la présence de toxines.

Diversité

La diversité définit de façon simple et synthétique, bien qu'incomplète, la structure d'une communauté. De ce fait, cette variable est fréquemment utilisée pour comparer différents échantillons, qu'ils proviennent de la même localité (variation annuelle) ou de différentes régions (variation spatiale).

Les indices de diversité sont divers et variés (voir MARGALEFF, 1977 et MAGURRAN, 1988) ; en général, ils prétendent établir la richesse en espèces d'une communauté, en relation avec une unité d'échantillonnage. Du fait de sa facilité de calcul et son utilisation répandue (ce qui permet de comparer les résultats de divers travaux), nous avons employé l'indice de Shannon (SHANNON-WEAVER, 1957).

Tableau 5
Relation par mois des espèces les plus abondantes

	Mois :	1	2	3	4	5	6	7	8	9	10	11	12
Cossidae	*P. caestrum*	-	-	-	5	-	-	-	-	-	-	-	-
	D. ulula	-	-	-	-	9	8	-	-	-	-	-	-
Lasiocampidae	*T. ilicis*	-	-	7	-	-	-	-	-	-	-	-	-
	M. castrensis	-	-	-	-	-	10	4	-	-	-	-	-
	L. trifolii	-	-	-	-	-	-	-	-	9	-	-	-
Sphingidae	*L. populi*	-	-	-	-	6	-	-	-	-	-	-	-
	D. porcellus	-	-	-	-	-	5	-	-	-	-	-	-
Geometridae	*L. clavaria*	-	-	-	-	-	-	-	-	-	-	10	-
	Ch. rufata	-	5	10	-	-	-	-	-	-	-	-	-
	A. pantaria	-	-	-	-	-	-	-	-	4	-	-	-
	T. murinaria	-	-	-	-	-	-	-	9	-	-	-	-
	C. pennaria	6	-	-	-	-	-	-	-	-	-	-	9
	B. strataria	-	-	8	-	-	-	-	-	-	-	-	-
	Ch. caliginearia	2	2	5	-	-	-	-	-	-	-	-	-
	A. ochrearia	-	-	-	-	8	-	-	-	-	-	-	-
Thaumetopoeidae	*Th. pityocampa*	-	-	-	-	-	-	9	6	-	-	-	-
Notodontidae	*C. iberica*	-	-	-	8	-	-	-	-	-	-	-	-
	Ph. tremula	-	-	-	10	-	-	-	-	-	-	-	-
Lymantriidae	*L. dispar*	-	-	-	-	-	-	5	10	-	-	-	-
Arctiidae	*E. complana*	-	-	-	-	-	-	8	1	10	-	-	-
	E. caniola	-	-	-	-	-	3	6	7	2	4	-	-
	E. pygmaeola	-	-	-	-	-	-	-	2	-	-	-	-
	Ph. fuliginosa	-	-	-	2	3	1	1	4	1	-	-	-
	C. pudica	-	-	-	-	-	-	-	-	3	-	-	-
	S. lubricipeda	-	-	-	-	4	4	-	-	-	-	-	-
	D. mendica	-	-	-	1	2	-	-	-	-	-	-	-
Noctuidae	*T. luctuosa*	-	-	-	-	-	-	6	5	8	-	-	-
	E. trabealis	-	-	-	-	-	-	2	3	5	-	-	-
	A. lucida	-	-	-	-	-	-	10	8	-	-	-	-
	P. cinnamomea	-	5	-	-	-	-	-	-	-	-	-	-
	E. ochroleuca	-	-	-	-	-	-	3	-	-	-	-	-
	L. testacea	-	-	-	-	-	-	-	-	-	5	-	-

	Mois :	1	2	3	4	5	6	7	8	9	10	11	12
Noctuidae	*Rh. lutosa*	-	-	-	-	-	-	-	-	-	-	8	-
	H. ambigua	-	-	-	-	-	7	-	-	6	6	-	-
	S. fixa	-	-	-	-	-	6	-	-	-	-	-	-
	A. nigra	-	-	-	-	-	-	-	-	-	7	7	10
	X. exsoleta	-	3	-	-	-	-	-	-	-	-	-	-
	X. areola	-	-	8	-	-	-	-	-	-	-	-	-
	V. jaspidea	-	-	4	6	-	-	-	-	-	-	-	-
	T. jodea	-	-	-	-	-	-	-	-	-	9	-	-
	C. alicia	1	1	2	-	-	-	-	-	-	-	5	3
	C. daubei	-	-	-	-	-	-	-	-	-	-	-	5
	C. torrida	-	4	-	-	-	-	-	-	-	-	-	-
	A. lota	4	-	-	-	-	-	-	-	-	-	9	4
	A. blidaensis	-	-	-	-	-	-	-	-	-	-	-	8
	A. lychnidis	3	-	-	-	-	-	-	-	-	2	1	1
	O. lunosa	-	-	-	-	-	-	-	-	-	1	4	-
	X. ocellaris	-	-	-	-	-	-	-	-	-	8	-	-
	L. oleracea	-	-	-	-	-	9	-	-	-	-	-	-
	E. conspicillaris	-	-	-	9	-	-	-	-	-	-	-	-
	O. gracilis	-	-	-	3	-	-	-	-	-	-	-	-
	O. cerasi	-	5	-	-	-	-	-	-	-	-	-	-
	O. incerta	-	5	1	10	-	-	-	-	-	-	-	-
	O. gothica	-	-	3	6	-	-	-	-	-	-	-	-
	M. albipuncta	-	-	-	-	10	-	-	-	-	-	-	-
	M. vitellina	-	-	-	-	1	2	-	-	-	-	-	-
	M. unipuncta	-	-	-	-	-	-	-	-	-	-	2	2
	M. sicula	-	-	-	4	5	-	-	-	-	-	-	-
	A. ipsilon	-	-	-	-	-	-	-	-	-	-	-	5
	O. plecta	-	-	-	-	6	-	-	-	-	-	-	-
	N. pronuba	-	-	-	-	-	-	-	-	-	-	6	-
	P. glareosa	-	-	-	-	-	-	-	-	-	10	-	-
	P. saucia	4	-	-	-	-	-	-	-	-	-	-	5
	X. c -nigrum	-	-	-	-	-	-	-	-	-	-	3	-
	X. xanthographa	-	-	-	-	-	-	-	-	7	2	-	-
	C. rubricosa	-	-	6	-	-	-	-	-	-	-	-	-

$$H = \sum_{i=1}^{s} \left[\frac{n_i}{n} * \log_2 \frac{n_i}{n} \right]$$

H = Indice de Shannon.
n_i = Nombre d'individus de l'espèce **i**.
n = Nombre total d'individus capturés.
s = Nombre total d'espèces capturées.

L'analyse de la diversité annuelle dans les différentes localités de capture (Tableau 6) révèle des valeurs très élevées, ce qui indique que les communautés de lépidoptères que l'on y observe sont relativement stables malgré une importante disproportion dans les taux d'abondance. En effet, la plupart des espèces capturées sont rares ou très rares et seule une infime minorité peut être considérée comme abondante (Tableau 7).

Vingt-cinq des trente échantillons considérés et appartenant aux 19 localités étudiées, présentent un indice supérieur à quatre.

Tout au long de l'année, la diversité fluctue de différente façon, selon la localité considérée (Tableau 6). En général, la diversité augmente de janvier à juin ou juillet, se stabilise ou diminue légèrement en été, recommence à augmenter au début de l'automne et diminue brusquement en novembre.

Si l'on réorganise les données du tableau 6 de sorte que n'apparaissent que les trois mois pour lesquels l'indice de Shannon est le plus élevé, on obtient le tableau 8 dans lequel ne figurent plus que dix-neuf échantillons (provenant de quinze localités). Par exemple, dans la première ligne du tableau, le numéro huit indique que pour la localité de Lecároz et pour l'échantillonnage de 1983, le mois d'août présente l'indice de Shannon le plus élevé, suivi par les mois de juin et mai. On note qu'en octobre la diversité est maximale dans la plupart des localités (sept sur dix-neuf) ; viennent ensuite les mois de juin et juillet, puis mai, août et septembre. Aucun des autres mois ne présente jamais de valeur maximale pour l'indice de Shannon. Pour les localités du nord de Navarre, la diversité maximale est atteinte en été et au début de l'automne alors que dans de nombreuses localités du sud (Ribera), les valeurs les plus élevées sont obtenues à la fin du printemps, bien qu'elles restent élevées jusqu'en automne (octobre).

Si l'on met en relation ces données avec l'incorporation à l'ensemble, de la nombreuse communauté des Noctuides, en particulier Hadeninae, avec vol printanier, et Cuculliinae et Noctuinae, dont le vol est automnal, on peut dire que les valeurs maximales de l'indice de Shannon, à la fin du printemps se justifient par l'apparition essentiellement de la première génération (et parfois la seule) des Hadeninae. Le maximun automnal doit être lié à l'émergence des Cuculliinae et des Noctuinae, avec lesquelles coïncident en plus les espèces qui ont subi une diapause estivale. Le maintien d'une diversité élevée pendant l'été et au début de l'automne dans la région nord doit être lié tant à la longueur et à la rudesse de l'hiver qu'à la relative douceur de l'été, alors que dans la région de la Ribera, caractérisée par un été chaud et sec, la diversité chutera dès juillet.

Les douze échantillons de plus grande diversité sont, dans l’ordre :

Ilundáin 1984	(Rouvraie)	6’15
Marcilla 1985	(Forêt de chêne Kermès)	6’06
Larraga 1985	(Forêt de chêne vert)	5’91
Mendavia 1984	(Forêt de chêne Kermès)	5’83
Sartaguda 1985	(Forêt de chêne Kermès)	5’81
Lecároz 1983	(Chênaie)	5’76
Ilundáin 1983	(Rouvraie)	5’70
Ucar 1986	(Rouvraie)	5’63
Buñuel 1984	(Forêt de chêne Kermès)	5’62
La Oliva 1985	(Forêt de chêne vert)	5’58
Fontellas 1985	(Forêt de chêne Kermès)	5’51
Ucar 1987	(Rouvraie)	5’41

Comme l’indique la liste ci-dessus, rouvraie, forêt de chêne Kermès et forêt de chêne vert, sont les formations végetales présentant la plus grande diversité. L’échantillon annuel le plus riche a été observé à Ilundáin en 1984, dans le domaine du *Quercus faginea* et présentait une diversité réellement élevée (6´15 bits/individus), avec 290 espèces. Ce résultat concorde avec ceux obtenus pour Papilionoidea et Hesperioidea dans le centre de la Péninsule Ibérique (VIEJO, 1985 ; VIEJO *et al.*, 1989), qui révélaient une importante diversité dans les forêts de chêne vert. Cependant, si l’on calcule la diversité globale des formations végétales, les forêts de chêne vert sont les plus riches, mais suivies de près par les rouvraies et les forêts de chêne Kermès ; quoi qu’il en soit les rouvraies sont celles qui présentent le plus grand nombre d’espèces (378).

Chênaie	5’76 (85 esp.)
Hêtraie	4’73 (66 esp.)
Rouvraie	6’31 (378 esp.)
Forêt de chêne vert	6’54 (355 esp.)
Forêt de chêne Kermès	6’29 (331 esp.)

L’analyse de l’équitabilité dans les différentes localités (Tableau 6) indique une diminution au cours de l’été, que l’on attribue à la diminution de la diversité par rapport au maximum possible, en tenant compte du nombre d’espèces obtenues.

Conclusions

La Navarre est une région riche en macrohétérocères ; nous y avons capturé 651 espèces de 14 familles, ce qui représente 44,9% des espèces ibériques.

Les localités les plus riches se situent dans le domaine climatique des chênaies (*Quercus*), en particulier les chênes verts, chênes rouvres et chênes Kermès. Bien que la plupart des localités soient situées en zones agricoles, cette activité ne semble pas altérer de façon importante la structure des communautés de macrohétérocères si l’on s’en tient aux valeurs de l’équitabilité, supérieures en général à 0,75, ce qui signifie que la diversité réelle est proche du maximum.

Tableau 6

Indice de Shannon et équitabilité de chaque localité,leur variation tout au long de l'année
Saisons : **H** : Hiver (J+F+M). **Pr** : Printemps (A+M+J). **E** : Été (J+A+S). **Au** : Automne (O+N+D)

	J	F	M	**H**	A	M	J	**Pr**	J	A	S	**E**	O	N	D	**Au**	Annuel
Lecároz 1983																	
Shannon	-	-	-	-	-	3,49	4,38	**4,72**	-	5,17	-	**5,25**	3,03	2,56	-	**3,10**	5,76
Équitabilité	-	-	-	-	-	0,92	0,92	**0,91**	-	0,94	-	**0,94**	0,91	0,71	-	**0,76**	0,90
N° d'individus	-	-	-	-	-	24	55	**79**	4	103	-	**107**	25	34	-	**59**	245
N° d'espèces	-	-	-	-	-	14	27	**36**	4	46	-	**49**	10	12	-	**17**	85
Imoz 1986																	
Shannon	-	-	-	-	-	-	-	-	-	4,03	4,00	**4,65**	-	-	-	-	4,73
Équitabilité	-	-	-	-	-	-	-	-	-	0,73	0,82	**0,78**	-	-	-	-	0,78
N° d'individus	-	-	-	-	-	-	13	-	-	200	118	**318**	-	-	-	-	331
N° d'espèces	-	-	-	-	-	-	8	-	-	45	30	**62**	-	-	-	-	66
Ilundáin 1983																	
Shannon	-	-	-	-	2,27	3,05	4,80	**5,04**	4,31	3,72	4,87	**5,08**	4,95	3,62	3,53	**5,12**	5,70
Équitabilité	-	-	-	-	-	0,88	0,83	**0,84**	0,80	0,62	0,74	**0,71**	0,89	0,78	0,88	**0,86**	0,75
N° d'individus	-	-	-	-	6	21	225	**25**	182	798	815	**1795**	154	90	39	**283**	2330
N° d'espèces	-	-	-	-	5	11	56	**63**	42	62	97	**145**	48	25	16	**62**	197
Ilundáin 1984																	
Shannon	-	-	-	-	4,11	-	4,98	**5,52**	5,72	5,00	5,33	**5,80**	4,92	4,59	-	**5,13**	6,15
Équitabilité	-	-	-	-	0,91	-	0,87	**0,89**	0,81	0,70	0,76	**0,74**	0,84	0,90	-	**0,84**	0,75
N° d'individus	-	-	-	-	47	17	163	**227**	1398	1846	1300	**4544**	249	74	13	**336**	5107
N° d'espèces	-	-	-	-	23	14	53	**74**	136	138	132	**231**	58	34	9	**68**	289
Ucar 1986																	
Shannon	-	-	-	-	-	-	-	-	4,21	-	4,87	**5,26**	4,57	2,10	-	**4,49**	5,63
Équitabilité	-	-	-	-	-	-	-	-	0,74	-	0,75	**0,76**	0,81	0,46	-	**0,76**	0,78
N° d'individus	-	-	-	-	-	-	-	-	410	4	658	**1072**	314	134	-	**448**	1519
N° d'espèces	-	-	-	-	-	-	-	-	51	3	91	**123**	51	24	-	**61**	152
Ucar 1987																	
Shannon	-	-	-	-	3,87	4,42	-	**4,70**	4,63	-	-	-	-	-	-	-	5,41
Équitabilité	-	-	-	-	0,82	0,82	-	**0,80**	0,85	-	-	-	-	-	-	-	0,84
N° d'individus	-	-	-	-	85	129	-	**214**	167	-	-	-	-	-	-	-	381
N° d'espèces	-	-	-	-	26	42	-	**58**	43	-	-	-	-	-	-	-	87

	J	F	M	**H**	A	M	J	**Pr**	J	A	S	**E**	O	N	D	**Au**	Annuel
Arizala 1986																	
Shannon	-	-	-	-	-	-	3,11	**2,66**	4,41	3,55	4,25	**5,24**	-	-	-	**2,54**	5,39
Équitabilité	-	-	-	-	-	-	0,90	**0,77**	0,77	0,78	0,76	**0,80**	-	-	-	**0,65**	0,81
N° d'individus	-	-	-	-	-	13	19	**32**	288	93	244	**625**	18	6	28	**52**	708
N° d'espèces	-	-	-	-	-	1	11	**11**	54	23	48	**92**	12	2	3	**15**	100
Arizala 1987																	
Shannon	-	-	-	-	3,79	3,94	2,73	**4,37**	-	-	-	-	-	-	-	-	4,37
Équitabilité	-	-	-	-	0,84	0,86	0,65	**0,77**	-	-	-	-	-	-	-	-	0,77
N° d'individus	-	-	-	-	61	69	104	**234**	1	-	-	-	-	-	-	-	235
N° d'espèces	-	-	-	-	23	24	18	**50**	1	-	-	-	-	-	-	-	51
Azcona 1986																	
Shannon	-	-	-	-	-	-	4,66	-	-	-	-	-	-	-	-	-	-
Équitabilité	-	-	-	-	-	-	0,78	-	-	-	-	-	-	-	-	-	-
N° d'individus	-	-	-	-	-	-	351	-	-	-	-	-	-	-	-	-	-
N° d'espèces	-	-	-	-	-	-	63	-	-	-	-	-	-	-	-	-	-
Oteiza 1986																	
Shannon	-	-	-	-	-	-	3,92	-	3,57	3,01	3,64	**3,98**	-	2,30	-	**3,15**	4,20
Équitabilité	-	-	-	-	-	-	0,91	-	0,61	0,64	0,64	**0,60**	-	0,69	-	**0,81**	0,62
N° d'individus	-	-	-	-	-	-	50	-	984	249	500	**1733**	13	30	-	**43**	1826
N° d'espèces	-	-	-	-	-	-	20	-	56	26	53	**98**	10	10	-	**15**	112
Larraga 1985																	
Shannon	-	-	-	-	3,74	4,25	4,38	**5,20**	4,11	3,43	4,12	**4,99**	4,52	2,31	-	**4,08**	5,91
Équitabilité	-	-	-	-	0,90	0,89	0,84	**0,86**	0,78	0,71	0,76	**0,78**	0,83	0,49	-	**0,71**	0,81
N° d'individus	-	-	6	-	39	50	151	**240**	156	119	172	**447**	239	177	-	**416**	1109
N° d'espèces	-	-	3	-	18	27	37	**65**	38	29	42	**84**	44	27	-	**54**	157
Larraga 1986																	
Shannon	-	-	3,13	**3,17**	-	-	-	-	-	-	-	-	-	-	-	-	3,44
Équitabilité	-	-	0,87	**0,83**	-	-	-	-	-	-	-	-	-	-	-	-	0,84
N° d'individus	4	10	31	**45**	8	-	-	-	-	-	-	-	-	-	-	-	53
N° d'espèces	2	3	12	**14**	7	-	-	-	-	-	-	-	-	-	-	-	17

	J	F	M	**H**	A	M	J	**Pr**	J	A	S	**E**	O	N	D	**Au**	Annuel
Sangüesa 1983																	
Shannon	-	-	-	-	-	-	4,53	-	3,97	3,16	-	**3,67**	-	-	-	-	4,45
Équitabilité	-	-	-	-	-	-	0,82	-	0,84	0,64	-	**0,69**	-	-	-	-	0,73
N° d'individus	-	-	-	-	-	-	227	-	134	202	-	**336**	-	-	-	-	563
N° d'espèces	-	-	-	-	-	-	45	-	26	30	-	**39**	-	-	-	-	68
Cáseda 1985																	
Shannon	-	-	3,41	-	4,62	4,74	4,98	**5,75**	2,64	2,84	-	**3,22**	5,24	3,24	-	**4,76**	4,24
Équitabilité	-	-	0,72	-	0,89	0,84	0,79	**0,83**	0,71	0,71	-	**0,69**	0,87	0,66	-	**0,76**	0,56
N° d'individus	-	-	240	-	129	186	461	**776**	33	48	11	**92**	287	265	30	**582**	1690
N° d'espèces	-	-	27	-	36	50	78	**120**	13	16	8	**26**	64	30	4	**76**	195
Cáseda 1986																	
Shannon	1,70	2,02	2,61	**2,73**	-	-	-	-	-	-	-	-	-	-	-	-	2,90
Équitabilité	0,47	0,49	0,63	**0,55**	-	-	-	-	-	-	-	-	-	-	-	-	0,56
N° d'individus	111	116	97	**324**	12	-	-	-	-	-	-	-	-	-	-	-	336
N° d'espèce	12	17	18	**32**	7	-	-	-	-	-	-	-	-	-	-	-	37
Carcastillo 1986																	
Shannon	-	-	-	-	-	-	-	-	-	3,04	-	-	-	-	-	-	-
Équitabilité	-	-	-	-	-	-	-	-	-	0,50	-	-	-	-	-	-	-
N° d'individus	-	-	-	-	-	-	-	-	5	687	-	-	-	-	-	-	692
N° d'espèces	-	-	-	-	-	-	-	-	4	66	-	-	-	-	-	-	68
Carcastillo 1987																	
Shannon	-	-	-	-	-	2,51	2,80	**2,82**	3,98	-	-	-	-	-	-	-	4,09
Équitabilité	-	-	-	-	-	0,51	0,74	**0,55**	0,79	-	-	-	-	-	-	-	0,68
N° d'individus	-	-	-	-	-	181	70	**251**	213	-	-	-	-	-	-	-	464
N° d'espèces	-	-	-	-	-	31	14	**36**	33	-	-	-	-	-	-	-	63
La Oliva 1985																	
Shannon	-	-	2,92	-	4,06	3,74	4,13	**4,70**	3,83	4,27	3,27	**4,41**	4,79	2,47	-	**4,68**	5,58
Équitabilité	-	-	0,92	-	0,77	0,70	0,73	**0,72**	0,66	0,78	0,66	**0,68**	0,84	0,58	-	**0,80**	0,75
N° d'individus	-	-	15	-	106	215	296	**617**	391	279	276	**946**	301	126	-	**427**	2005
N° d'espèces	-	-	9	-	38	41	51	**91**	55	45	31	**89**	51	19	-	**57**	174

	J	F	M	**H**	A	M	J	**Pr**	J	A	S	**E**	O	N	D	**Au**	Annuel
La Oliva 1986																	
Shannon	-	1,06	2,81	**2,88**	3,76	-	-	-	-	-	-	-	-	-	-	-	3,79
Équitabilité	-	0,53	0,78	**0,72**	0,89	-	-	-	-	-	-	-	-	-	-	-	0,79
N° d'individus	10	28	37	**75**	36	-	-	-	-	1	-	-	-	-	-	-	112
N° d'espèces	4	4	12	**16**	19	-	-	-	-	1	-	-	-	-	-	-	28
Mendavia 1984																	
Shannon	-	-	-	-	-	-	5,45	-	4,85	4,76	4,32	**5,11**	4,72	-	-	-	5,83
Équitabilité	-	-	-	-	-	-	0,85	-	0,76	0,84	0,79	**0,76**	0,81	-	-	-	0,80
N° d'individus	-	-	-	-	-	-	333	-	506	266	236	**1008**	263	-	-	-	1604
N° d'espèces	-	-	-	-	-	-	83	-	84	51	45	**109**	57	-	-	-	161
Sartaguda 1984																	
Shannon	-	-	-	-	-	-	3,68	**3,93**	4,09	4,14	3,78	**4,22**	3,90	4,00	2,94	**4,59**	4,89
Équitabilité	-	-	-	-	-	-	0,77	**0,80**	0,87	0,72	0,63	**0,65**	0,74	0,83	0,77	**0,78**	0,69
N° d'individus	-	-	-	-	7	-	63	70	73	362	666	**1101**	147	114	46	**307**	1478
N° d'espèces	-	-	-	-	5	-	27	30	26	53	65	**92**	39	28	14	**58**	133
Sartaguda 1985																	
Shannon	-	-	3,72	-	3,51	3,23	4,63	**4,73**	4,23	3,71	3,88	**4,81**	3,69	2,75	-	**3,83**	5,81
Équitabilité	-	-	0,93	-	0,84	0,85	0,86	**0,81**	0,85	0,81	0,97	0,84	0,94	0,69	-	**0,80**	0,84
N° d'individus	-	-	26	-	30	44	108	**182**	74	72	20	**166**	24	52	7	**83**	457
N° d'espèces	-	-	16	-	18	14	41	**56**	31	24	16	**53**	15	16	5	**28**	122
San Adrián 1984																	
Shannon	-	-	-	-	-	-	3,14	**3,29**	3,96	3,64	4,52	**4,88**	4,35	-	-	-	5,13
Équitabilité	-	-	-	-	-	-	0,68	**0,70**	0,68	0,89	0,82	**0,74**	0,90	-	-	-	0,75
N° d'individus	-	-	-	-	33	-	157	**190**	370	39	143	**552**	89	-	-	-	831
N° d'espèces	-	-	-	-	2	-	24	**26**	58	17	45	**94**	29	-	-	-	115
Marcilla 1985																	
Shannon	-	-	3,01	-	4,17	5,08	4,62	**5,25**	3,31	4,76	4,70	**5,06**	4,96	3,26	-	**4,81**	6,06
Équitabilité	-	-	0,84	-	0,87	0,86	0,75	**0,78**	0,66	0,86	0,82	**0,79**	0,79	0,66	-	**0,75**	0,80
N° d'individus	-	-	28	-	87	270	422	**779**	124	193	222	**539**	611	278	6	**895**	2241
N° d'espèces	-	-	12	-	28	60	71	**105**	33	47	52	**84**	**76**	30	4	**83**	197

	J	F	M	**H**	A	M	J	**Pr**	J	A	S	**E**	O	N	D	**Au**	Annuel
Marcilla 1986																	
Shannon	-	-	2,73	**2,38**	3,29	-	-	-	-	-	-	-	-	-	-	-	-
Équitabilité	-	-	0,86	**0,66**	0,92	-	-	-	-	-	-	-	-	-	-	-	-
N° d'individus	22	20	32	**74**	23	-	-	-	-	-	-	-	-	-	-	-	97
N° d'espèces	4	5	9	**12**	12	-	-	-	-	-	-	-	-	-	-	-	-
Cadreita 1983																	
Shannon	-	-	-	-	-	4,04	3,70	**4,24**	4,05	3,84	-	**4,39**	4,49	-	-	**4,49**	5,17
Équitabilité	-	-	-	-	-	0,87	0,86	**0,84**	0,87	0,78	-	**0,80**	0,84	-	-	**0,83**	0,80
N° d'individus	-	-	-	-	12	71	73	**156**	64	110	1	**175**	151	12	-	**163**	494
N° d'espèces	-	-	-	-	3	25	20	**33**	25	30	1	**45**	40	5	-	**42**	87
Cadreita 1984																	
Shannon	-	-	-	-	-	-	-	-	0,27	4,34	1,63	**4,74**	4,75	3,25	2,72	**4,43**	5,34
Équitabilité	-	-	-	-	-	-	-	-	0,06	0,79	0,33	**0,78**	0,81	0,68	0,79	**0,73**	0,79
N° d'individus	-	-	-	-	-	-	1	-	86	200	149	**435**	299	255	50	**604**	1040
N° d'espèces	-	-	-	-	-	-	1	-	29	46	31	**67**	59	28	11	**67**	108
Cadreita 1985																	
Shannon	-	-	-	-	3,58	3,80	-	**4,39**	-	3,10	3,71	**3,88**	4,29	2,36	-	**3,67**	5,12
Équitabilité	-	-	-	-	0,90	0,83	-	**0,84**	-	0,66	0,86	**0,73**	0,87	0,60	-	**0,72**	0,79
N° d'individus	-	1	6	-	37	52	12	**101**	4	121	44	**169**	77	91	2	**170**	447
N° d'espèces	-	1	5	-	16	24	9	**37**	4	26	20	**40**	31	15	2	**35**	90
Fontellas 1985																	
Shannon	-	-	-	-	3,91	4,45	4,26	**5,05**	2,25	-	-	-	-	3,56	-	**3,61**	5,51
Équitabilité	-	-	-	-	0,90	0,85	0,88	**0,85**	0,75	-	-	-	-	0,81	-	**0,80**	0,86
N° d'individus	-	-	-	-	**39**	94	69	**202**	19	-	-	-	10	83	-	**93**	314
N° d'espèces	-	-	-	-	20	38	29	**62**	8	-	-	-	2	21	-	**23**	83
Buñuel 1984																	
Shannon	-	-	-	-	-	-	-	-	5,00	4,72	4,82	**5,35**	-	4,07	-	-	5,62
Équitabilité	-	-	-	-	-	-	-	-	0,84	0,80	0,85	**0,80**	-	0,81	-	-	0,82
N° d'individus	-	-	-	-	-	-	-	-	405	409	223	**1037**	-	358	-	-	1395
N° d'espèces	-	-	-	-	-	-	-	-	63	61	52	**103**	-	32	-	-	113

Tableau 7

Degré d'abondance des espèces capturées

Degré d'abondance	Nombre d'espèces	Pourcentage n° d'espèces	Nombre d'individus	Pourcentage n° d'individus
>2000	1	0,15	2649	6,94
1001-2000	4	0,61	5666	14,84
501-1000	9	1,38	6350	16,64
251-500	21	3,22	7582	19,86
51-250	95	14,59	10389	27,22
26-50	72	11,05	2542	6,66
<26	449	68,97	2982	7,81
Total	651	99,97	38160	99,97

Tableau 8

Réarrangement des différents mois en fonction de leur importance pour l'indice de Shannon

Divisions géographiques de la Navarre : **Dt** : Division traditionnelle (M = Montagne. ZM = Zone moyenne. R= Ribera). **Ce** : Régions écologiques (Vc = Vallées cantabriques. Cc = Vallées centrales. Nr = Navarre moyenne orientale. R= Ribera).

Localité	Échantillon	Numéro d'ordre			Dt	Ce
		1°	2°	3°		
Lecároz	1983	8	6	5	M	Vc
Ilundáin	1983	10	9	6	M	Cc
Ilundáin	1984	7	9	8	M	Cc
Ucar	1986	9	10	7	ZM	Nr
Arizala	1986	7	9	8	ZM	Cc
Oteiza	1986	6	9	7	ZM	Nr
Larraga	1985	10	6	5	ZM	R
Cáseda	1985	10	6	5	ZM	R
La Oliva	1985	10	8	6	ZM	Nr
Mendavia	1984	6	7	8	R	R
Sartaguda	1984	8	7	11	R	R
Sartaguda	1985	6	7	9	R	R
San Adrián	1984	9	10	7	R	R
Marcilla	1985	5	10	8	R	R
Cadreita	1983	10	7	5	R	R
Cadreita	1984	10	8	11	R	R
Cadreita	1985	10	5	9	R	R
Fontellas	1985	5	6	4	R	R
Buñuel	1984	7	9	8	R	R

La famille qui a été le plus capturée est celle des Noctuides, lesquelles prédominent en automne et en hiver, bien qu'ils soient abondants en toute saison ; elle est suivie par celle des Arctiides, à cause en particulier de l'abondance de *Phragmatobia fuliginosa* au printemps et en été.

Il existe un ajustement entre les cycles biologiques des lépidoptères et la phénologie des plantes nourricières. Les espèces qui volent en hiver sont présentes au printemps au stade chenille, lesquelles s'alimentent de feuilles d'arbre (chênes, peupliers, saules, etc.) quand celles-ci sont le plus nutritives. Pour les espèces qui volent à partir du mois d'avril, les larves sont présentes en été et en automne et s'alimentent de plantes basses.

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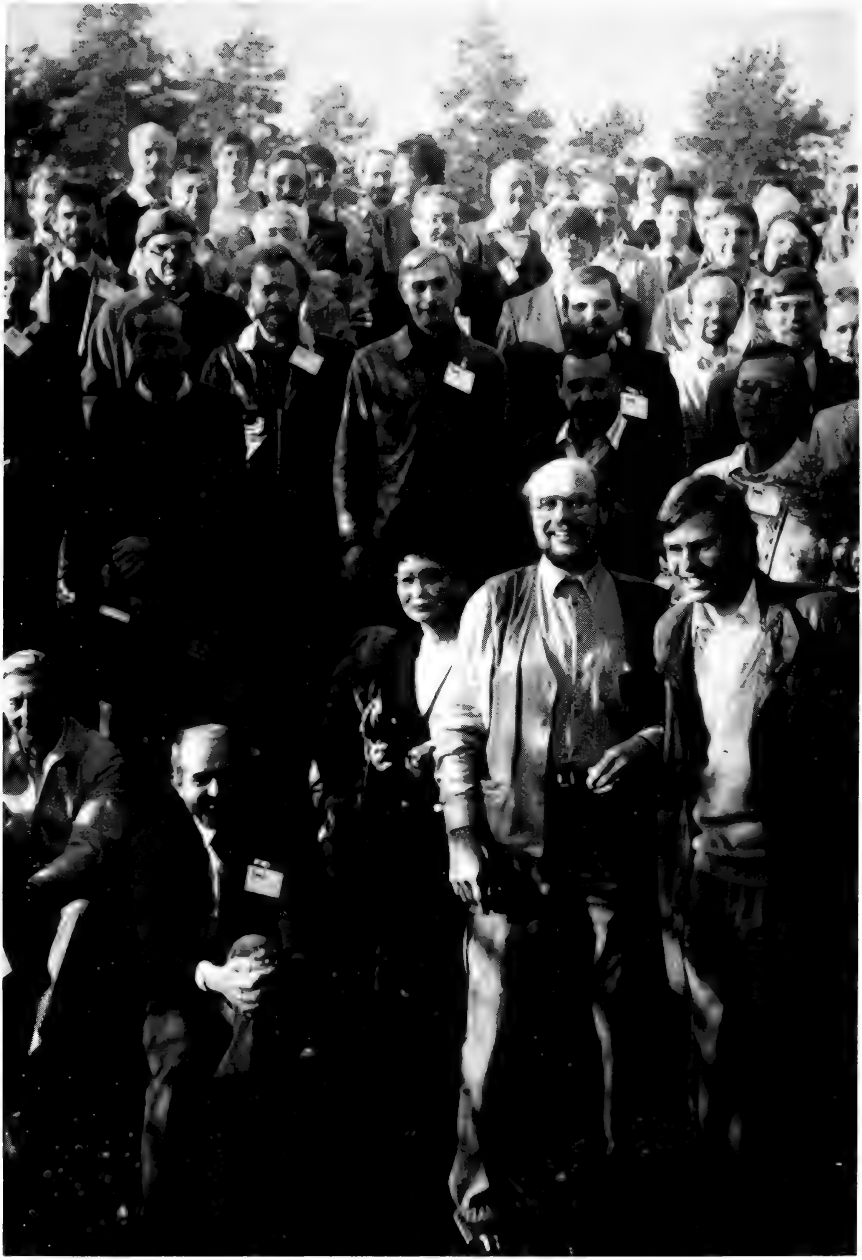

Some of the delegates at the 8th European Congress of Lepidopterology. Dr. Kauri Mikkola (Chairman of the Organising Committee) is standing at the front, second from the right. The President of SEL, Prof. Emilio Balletto (Turin), is sitting, second from the left, next to Dr. László Gozmány (Budapest), honorary member of SEL. Dr. Hansjürg Geiger (General Secretary of SEL) is standing front right. Photo : M. Sommerer.

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Biogeographical and ecological determinants of the central European peat bog Lepidoptera : The habitat island approach to conservation

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Summary

Oligotrophic peat bogs form characteristic habitat islands within the temperate forests of central Europe. These isolated relict bog ecosystems are similar to some subarctic and subalpine biomes ("edaphic forest-tundra") in being determined in the Holocene and by recent local ecology. The ecological determinants are interactions of suitable edaphic and climatic factors. Most of the tyrphobiontic and tyrphophilous Lepidoptera species have taxonomic affinities to boreal and subarctic zones. The "archipelago" of South Bohemian oligotrophic bogs is ideal for case studies, and model conservation projects.

Bog habitat island : outline of ecological history

Central European oligotrophic peat bogs (e.g. Mrtvý luh bog, Fig. 1) are isolated ecosystems similar in structure and function to subarctic wet forest-tundra (= "edaphic forest-tundra" sensu Hustich, 1957, see also Tuhkanen, 1984). In southern latitudes of the temperate forest zone, such peat bogs are characteristic azonal ecosystems, occurring in isolated and discrete patches in "average" landscape originally covered by forest. The habitat island development of most central European bogs, e.g. in South Bohemia, dates from the early Holocene (Jankovská, 1980) and the bogs became more acid and ombrotrophic during the Holocene ecological succession. The island-like characteristics have resulted from the interaction of both climatic and edaphic factors. Recently, the local cold/warm and wet/dry "continental" environment has been the main factor favouring the survival of relict cold adapted (stress tolerant and K-selected) biotas. Because of their different ecological histories each large bog is unique in its species composition (e.g. insects) and their taxonomic status (subspecies and geographical races). These central European oligotrophic bogs can be classified under the vegetation association : Pino rotundatae-Sphagnetum (see Neuhäusl, 1972 ; Spitzer, 1975 ; Mikkola & Spitzer, 1982, etc.). The linkage between insect community and vegetation

Fig. 1. The habitat island of Mrtvý luh bog, ca. 300 ha of edaphic "forest-tundra", Šumava Mts., 740 m.

association is very close, e.g. Lepidoptera associated with *Ledum palustre* (*Lyonetia ledi* Stt., *Olethreutes lediana* L., *Eupithecia gelidata* Möschl.) and *Vaccinium uliginosum* (*Anarta cordigera* Thnbg., *Lithophane lamda* F., *Colias palaeno* L.).

Ecological grouping of peat bog Lepidoptera : stenotopic species

1. Tyrphobionts (Peus, 1932 ; Spitzer, 1975 ; Roháček, 1982 ; Meineke, 1985 ; Mikkola & Spitzer, 1982 ; Gelbrecht, 1988, etc.) are obligatorily associated with peat bogs in temperate and southern boreal zones. Their most important ecological requirements are micro (meso) climatic and edaphic conditions (*Eugraphe subrosea* Steph. is a typical example, Fig. 2). Some bog Lepidoptera are closely associated with the habitat because of their foodplants (e.g. strictly monophagous species that feed on *Ledum palustre*, *Vaccinium uliginosum* and *Eriophorum vaginatum*). In some cases monophagy is recent, induced by the Holocene vegetation succession, which resulted in the extinction of certain plants (see Spitzer *et al.*, 1991 — *Eupithecia gelidata* Möschl.). There is a general trend to a weaker tyrphobiontic association towards the northern and alpine timber lines (Mikkola & Spitzer, 1982).

2. Tyrphophilous biotas are plants and animals that are not restricted to peat bogs. Such peatland species colonise other wetlands, wet forests, heathlands

Fig. 2. Larva of *Eugraphe subrosea* (Steph.), a local geographical race of the Mrtvý luh bog, Šumava Mts.

and meadows, but achieve their greatest population abundance in peat bogs (see Peus, 1932 ; Lepidoptera are listed by Spitzer, 1975 ; 1981 ; Mikkola & Spitzer, 1975 ; Gelbrecht, 1988).

Why is a peat bog "island" unique?

The recent habitat island structure of central European bogs is a unique product of the ecological succession in the Holocene. The relict biotas of bogs, plants and invertebrates especially, have lived here from the early Holocene or even the late Glacial stadials (Peus, 1932 ; Coope, 1970 ; Jankovská, 1980). Such organisms are very vulnerable to extinction because they do not occur in other habitats. Changes in the local environment (water level, chemistry of water and peat, etc.) of a peat bog can cause the extinction of the local tyrphobiontic taxa associated with a particular habitat island. Such changes are irreversible because it is not possible to recreate the evolutionary history that gave rise to the biodiversity of a specific bog. A good example is the recent fate of subalpine bogs in the Krkonoše Mountains, which 14 years ago were sprayed with insecticide to suppress a forest pest. The relict and endemic (subspecies) insect fauna probably disappeared (e.g. *Pachnobia alpicola* (Zett.) a tyrphophilous relict noctuid of the subalpine zone). The habitat is now irregularly colonised by some opportunistic insect species. Insecticides and other chemicals are likely to prove fatal to the existence of such tyrphobiontic insect communities.

Conclusions for conservation management

The best conservation strategy for peat bogs and their Lepidoptera communities is a "no action strategy" — other than preserve good hydrological conditions. Generally, the hydrology is the most important factor. The bog ecosystem is fragile and any human impact is likely to prove fatal for some components of the fauna and flora. Species of Lepidoptera are the best bioindicators. Monitoring of the hydrological and other environmental conditions is necessary, if a bog is situated in a predominantly man made landscape.

Rules for conservation of central European peat bogs :

1. Maintain the hydrological conditions that prevent successional change from wetland to closed pine forest. Wet edaphic "forest-tundra" formation appears to be the optimal state (see also Meineke, 1985).

2. Ban the use of chemicals (insecticides, herbicides, etc.) close to the localities.

3. Conserve all of the "habitat islands". For example, in the case of the unique "archipelago" of peat bogs in the Šumava Mountains (see Wells *et al.*, 1983 ; Spitzer, 1981) the whole archipelago needs to be conserved.

Scientific and educational values of peat bog communities of Lepidoptera

It is difficult to separate the "educational" from the purely "scientific" value of central European bogs. The following scientific and educational priorities should be included in the scientific conservation programme :

1. A model study of habitat islands and their relict Lepidoptera communities based on the theory of island biogeography.

2. The use of peat bogs as sites for testing s-selection (stress tolerant taxa) and r- and K-selection hypotheses.

3. Studies of relict endangered species of Lepidoptera and their subspecies.

4. Evolutionary differentiation of the insect populations within and between "archipelagos" of bogs (e.g. *Colias palaeno* L. and *Eugraphe subrosea* Steph.).

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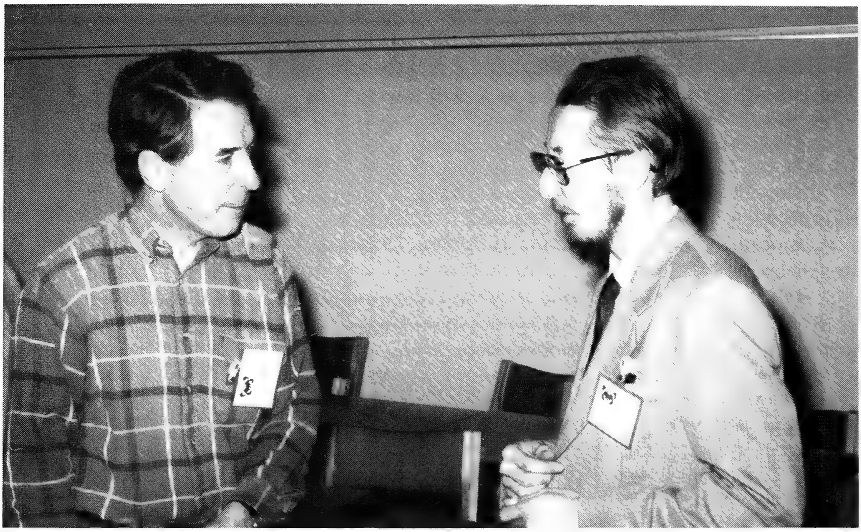
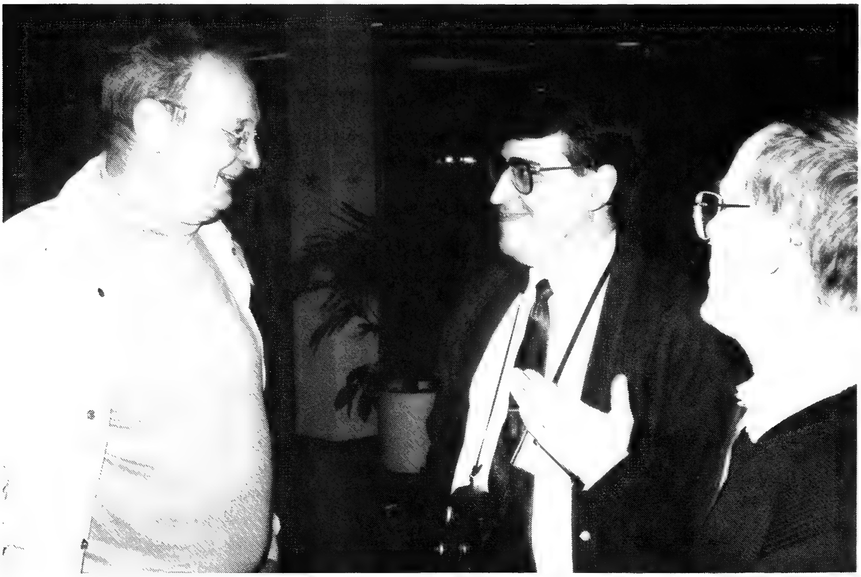


England meets Russia. David Agassiz (U.K.) discussing (presumably) the dynamics of *Phyllonorycter* populations with Michail Kozlov (Russia, at present in Finland). Photo : S. Whitebread.



Sweden meets Spain. Bengt Bengtsson (Sweden) introduces Ingvar Svensson (Sweden, left) to Antonio Vives Moreno (Spain). Photo : S. Whitebread.

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Conserving Britain's rarest moths

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Summary

The work of the Joint Nature Conservation Committee Moth Conservation Project has several components. The first involves servicing a national network of recorders which was set up in the winter of 1990/91 to trawl information on the current national distribution, status and conservation requirements of the rarer species of macro-moths in Britain. The information collected is being used to organise surveys and produce national surveys and produce national distribution maps, data sheets and a bibliography for the rarer moths. The rarer macro-moths have been defined as those species believed to occur in less than one hundred of the 10 km squares in Britain. Approximately 280 of the 730 or more macro-moth species that breed in Britain are in this category now. The collected information is used by the government conservation agencies to identify important breeding sites and advise on their management. Since its inception in 1987 the Moth Conservation Project has also been involved in devising and assisting practical conservation measures for a number of rare moths including six species of moths which receive legal protection in Britain and are listed on Schedule 5 of the Wildlife and Countryside Act 1981 and 1988 amendment. These six are *Zygaena viciae argyllensis* Tremewan, *Thetidia smaragdaria maritima* Prout, *Pareulype berberata* Denis & Schiffermüller, *Siona lineata* Scopoli, *Acosmetia caliginosa* Hübner and *Hadena irregularis* Hufnagel. Practical conservation measures for these species include site protection and defence, management work, ecological studies, captive breeding and translocation to establish new breeding colonies. The Moth Conservation Project also liaises with and promotes the work of a large number of other organisations and individuals involved in moth recording and conservation to raise public awareness and provide a national overview.

Introduction

This paper reports on the work of the Moth Conservation Project which was started by the Nature Conservancy Council (NCC) in 1987 and subsequently passed to one of its four successor organisations, the Joint Nature Conservation Committee (JNCC) following the reorganisation of the UK government conservation agency in April 1991. The JNCC is the UK government agency responsible for promoting nature conservation at the UK and international levels and is the coordinating body for the three separate country agencies of England (English Nature), Scotland (Scottish Natural Heritage) and Wales (Countryside Council for Wales). The author has been responsible for the Moth Conservation Project since its inception and the work has consisted of four main tasks. These are:

- — to identify which species are where, keep the information up to date and actively encourage recording effort ;
- — draw up a list of the species in greatest need of conservation ;
- — organise, coordinate and promote practical conservation measures ;
- — promote greater awareness of moths and other invertebrate animals and their value as indicators of habitat quality and change.

Details of these activities have been provided by WARING (1988a ; 1989a,b,c ; 1990a,b,c ; 1991a,b,c,d ; 1992a,b,c) and references contained therein. This paper is intended as a summary and guide.

Locating and documenting the resource

In Britain there is a long history of recording moth distribution and abundance. FUST (1868) provides an early account of the distribution of moths in Britain. More recently the late John Heath (based at the Biological Records Centre (BRC), Institute of Terrestrial Ecology, Monks Wood) organised a national recording scheme and this has formed the basis for the distribution maps which have been published in HEATH & EMMET (1976-1991). The recording scheme was discontinued due to lack of resources on the retirement of John Heath in 1982. There has been no decrease in the amount of voluntary recording effort however. The author estimates that several thousand light-traps are operated by private individuals and organisations each year in Britain and covering many more locations. There is a strong tradition of local recording which extends back more than two hundred years. For consistency local schemes are usually based on the Watsonian vice-county system which continues to be strongly advocated (MORRIS, 1990). Local lists continue to be published on a regular basis and often provide information on the habits and phenology of species. Increasingly the county lists are including distribution maps as well. CHALMERS-HUNT (1989) provides a recent bibliography of local lists. In addition the Rothamsted Insect Survey continues to maintain a network of nearly one hundred light-traps which are operated every night of the year throughout Britain. So far it has not been possible to set up a national recording scheme again that is capable of processing all the moth data that is being collected in Britain. At the same time conservation organisations frequently require greater detail about the occurrence of certain species than the basic grid reference and date class collected by John Heath's scheme. To provide the information required in conservation issues the

Nature Conservancy Council developed the Invertebrate Site Register (ISR) in 1979, with computerisation of the data-base from 1986 onwards. The ISR aims to maintain files on all UK sites of known invertebrate importance and to supply information about the species of conservation interest for use in site evaluation, protection, defence and management. Currently the ISR holds files on some 8500 sites. Many sources of information have been trawled to prepare short-lists of species which are nationally rare, restricted to particular habitats or are of conservation interest for some other reason, such as a population subject to long-term study. The ISR stores and retrieves this information. The data can be accessed by species rather than by site to allow compilation of a list of sites at which a particular species has been recorded or for production of a distribution map.

Hadley (1983 ; 1984) was the first to compile a list of the nationally scarce macro-moths. This was produced by using the BRC maps and by drawing on the experience of active field workers in the major British entomological societies. For the macro-moths, which may be regarded as those species included in Skinner (1984), the nationally scarce species were defined as those recorded since 1960 from less than one hundred of the 10km squares in the Ordnance Survey National Grid which covers the UK. This amounted to some 256 species. Hadley (1983) also drew on local lists to define additional species of regional interest. Since then information on these species has been entered on the ISR. A Red Data Book (Shirt, 1987), compiled at the same time and published in 1987, lists the species recorded from fifteen or fewer of the 10km squares and categorises these as endangered, vulnerable or rare on the basis of known threats to the sites in which they occur. This list includes 99 species or subspecies of macro-moths.

The Moth Conservation Project has been able to draw on the above publications and on the facilities and data in the ISR. The first step was to issue a list compiled from Hadley (1984) and Shirt (1987) and trawl in the data on these species from the years since 1980. This information has been used to compile up to date distribution maps and see if the species still merit their existing conservation status. Information on a further 80 localised species was also requested to assess whether any had moved into the nationally scarce category based on their status from 1980 onwards. The information was collected by contacting all existing county recorders, active field workers and by extracting records from the national entomological journals. In addition the Rothamsted Insect Survey kindly supplied copies of their records on disc and the Biological Records Centre have provided their data which enables comparison of distributions pre- and post-1980. At the time of writing, virtually all the data required for production of maps of the scarce species has been entered onto computer and maps such as Fig. 1 are being prepared for circulation to recorders for checking. This new generation of maps uses 1980 onwards to distinguish recent records and larger spot sizes to indicate multiple records of adults from the same 10 km square or evidence of breeding such as reports of immature stages. This is intended to focus attention on breeding colonies and distinguish them from records which may refer to vagrant specimens. The current generation of recorders is not in the habit of sending in details of numbers of moths seen and is mainly oriented to work with light-traps but it is hoped that the new maps will promote valuable work on larvae. At present it is true to say that much more information is being collected from the field than the national organisations are capable of trawling and processing and that the latter have been the weak link in the chain. During 1992 it is intended that an Atlas of up to date distribution maps and an accompanying text will be prepared for JNCC. This will make available the information collected so far.

Preparation of a list of nationally scarce macro-moths

The new maps will be used to define the current nationally scarce species. It is quite clear from the results that some species have increased and others have declined in range dramatically in the last ten years, even allowing for possible differences in recording effort and coverage. A good example is that of *Thera juniperata.* Since the last distribution map of this species was published (in Ward, 1977), *T. juniperata* has extended its range greatly, in part dispersed as immature stages on young juniper bushes (*Juniperus* spp.) which have become popular with gardeners in the Midland counties and elsewhere (Waring, 1992b). The current situation (Fig. 1) is very different from the mid-1970s and before, when *T. juniperata* was largely confined to parts of Scotland and to the chalk of south-eastern England. Some species have expanded their ranges greatly over the same time span, such as *Rhyacia simulans*, with no apparent assistance from man, while others have declined. Published map information and recording effort has sometimes proved to be a less than adequate indication of the real situation. The map of *Cucullia lychnitis* in Heath & Emmet (1983) shows records from only three 10 km squares in mainland Britain since 1960. A survey of this species in 1991 (Waring, 1992c) discovered post-1960 records from several other localities and that the species has bred in at least sixteen 10 km squares since 1980. It was found to be occupying almost all of these in 1991.

Practical conservation measures for nationally scarce species

National reviews and mapping projects are on-going but can become ends in themselves. The purpose of NCC and JNCC involvement has always been to use these as tools to launch and sustain practical conservation measures for the species in greatest need. When the Moth Conservation Project was started in 1987 the rarest species of macro-moth had already been identified and five of the species listed in Shirt (1987) as endangered had been given legal protection from collection and sale since 1981 under the terms of Schedule 5 of the Wildlife and Countryside Act of 1981. A sixth species had been proposed for inclusion in the quinquennial review of 1986 and was added in an amendment to the Act in 1988. A first priority in 1987 was to investigate the current status of the protected species on the ground.

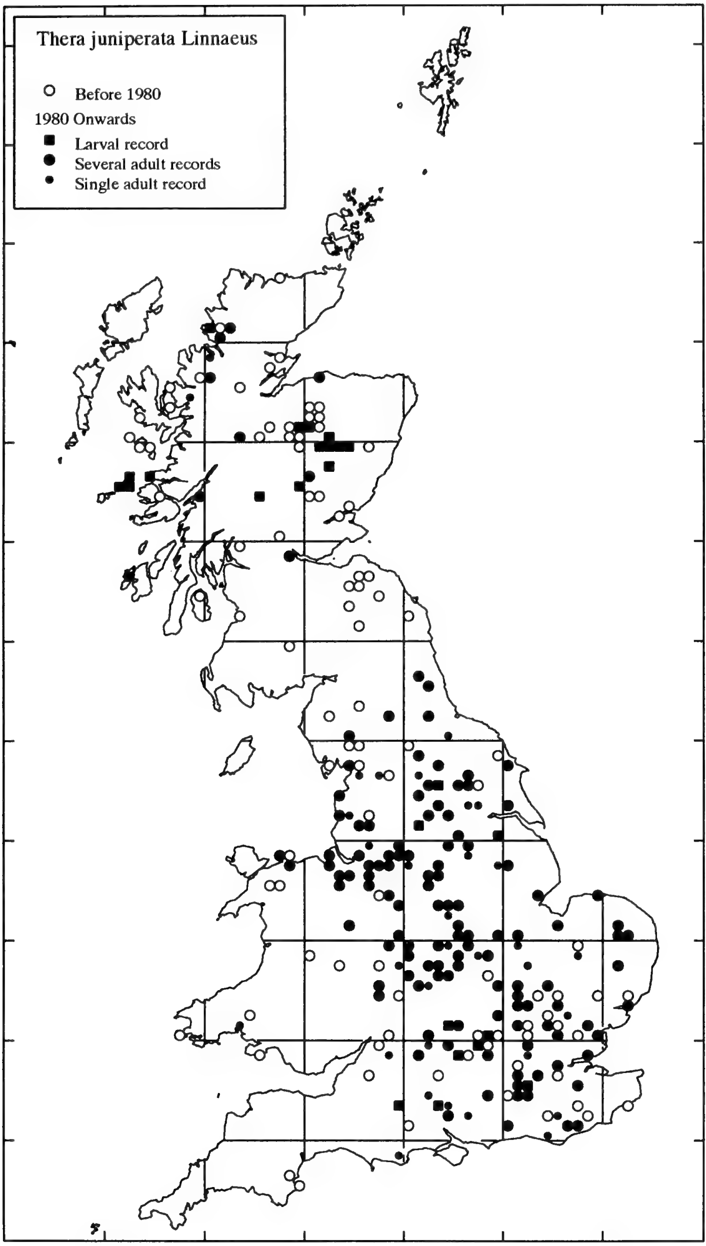

Fig. 1. The distribution of *Thera juniperata* L. in Britain.

Siona lineata

Within weeks of starting the post, work commenced on *Siona lineata*. This species is now confined in Britain to two fields of rank grassland in Kent although in the past it was more widespread (Waring, 1988a ; 1990a). The local NCC office had been sent a copy of a paper in draft which had been submitted to a leading British entomological journal by a highly respected entomologist complaining about the mis-management of part of one of the two remaining sites which is a National Nature Reserve. Sheep had been allowed to hard-graze part of the site and had reduced the turf height to less than 2 cm. which entomologists consider is much too short to provide suitable conditions for the moth to breed. Meetings were held with the regional staff responsible for the reserve and with the author of the draft. It soon became clear that although numbers of the adult moth had been counted annually since 1976 on a transect walk used for monitoring butterfly populations on the site, the ecological requirements of the moth and its immature stages were poorly known. The larval food-plant in the wild was generally considered to be *Brachypodium pinnatum*, upon which wild females had been seen laying and it was also considered that the tussocks of this plant probably provided important over-wintering refuges for the larvae. These impressions have had major implications when determining and reviewing the management of the site. The hard-grazing of part of the site had been an accident caused when sheep were penned there because of problems with stray dogs elsewhere on the site. In other parts of the reserve *B. pinnatum* was rampant to the virtual exclusion of other herbs and grasses. The moth was now absent from the hard-grazed site and dwindling in numbers elsewhere for unknown reasons.

Other entomologists were contacted immediately and it became apparent that no one had reared *S. lineata* successfully in captivity in Britain, at least not recently, in spite of several attempts supplying both grasses and dicotyledonous herbs. A literature search suggested that the latter was the more likely pabulum (e.g. Scorer, 1913 ; Skou, 1986). Field observations that summer confirmed the habit of ovipositing on *B. pinnatum* and other grasses and some eggs were collected for rearing. In a choice experiment newly hatched larvae were offered the range of common herbs available at the breeding site. From these they selected *Origanum vulgare* upon which they proceeded to develop. As the larvae grew in size they were transferred to as near natural conditions as possible, using potted turves from the site. The potted turves were enclosed in nets out of doors and the larvae were released into these before the winter to study their habits. Overwintering was successful and seven larvae were reared to adult on *O. vulgare*. Subsequently larvae have been found in the wild in association with damaged leaves of *O. vulgare* upon which they have fed. *B. pinnatum* appears to be important in providing daily roosting and basking sites for the larvae, which match the dry stems in colour, and in providing spinning sites for the zygaenid-like spindle-shaped cocoon this species produces. Full details and photographs of this work are given in Waring (1988a ; 1989a and 1990a).

Following the ecological work, the management of the parts of the site which the moth occupies has been modified to create a balance between sufficient *B. pinnatum* and abundant *O. vulgare*. In 1991 numbers of adult moths counted on the transect walk were higher than in any year since 1979 (Fig. 2), although this is probably the result of the dry weather and high temperatures experienced in 1990/91 as well as the management.

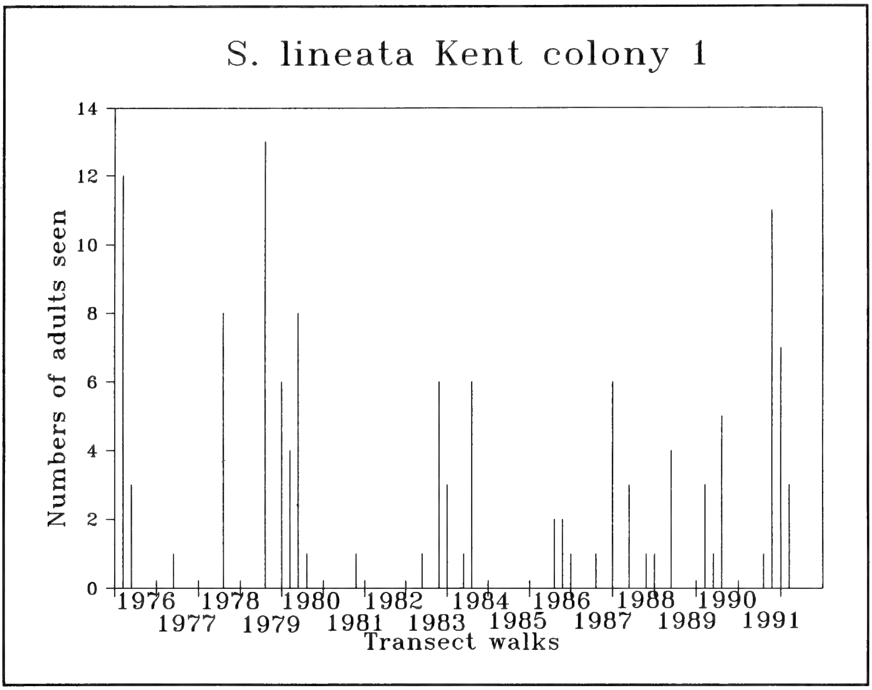

Fig. 2. The number of *Siona lineata* Scop. adults seen at one of the two known localities in Britain between the years 1976 and 1991.

Other work on *S. lineata* during the project has included monitoring the effects of an accidental fire which burned 10% of the site of the second remaining colony. It has been demonstrated that the moth will recolonise an area burned in May as early as the growing season of the following year, at which time adults have been seen ovipositing and the resulting larvae located later in the year. Searches for the moth in other fragments of rank chalk grassland elsewhere in Kent and in possible former localities in Dorset and Somerset have been organised but the moth has been found at none. Management to recover a former site in Kent at which the moth occurred up to 1984 has been set in motion and the second of the two known colonies has been scheduled a Site of Special Scientific Interest (SSSI) which confers a measure of protection from changes in land use under the terms of the Wildlife and Countryside Act 1981.

All five of the other Schedule 5 protected species have been given attention.

Acosmetia caliginosa

A. caliginosa had not been seen since 1984 and seems to have died out from both of its last known sites which were the edges of rides in conifer plantations on the Isle of Wight. The moth was described in NCC files as a creature of woodland rides and requiring sensitive ride-side management. Surveys for the moth were organised in 1987 (for larvae) and 1988 (for adults) and these covered former sites and a number of others known to support the larval food-plant *Serratula tinctoria*. A strong colony of the moth was discovered surviving on a site from which it had been reported nearly forty years previously and the breeding grounds were found to extend into a neighbouring property (WARING, 1990a,b). Both of these sites are open heathland and the larvae have since been found on plants of *S. tinctoria* growing in full sun amongst sparse vegetation — a much drier and warmer situation than the lush conditions which now exist in the edges of the plantation rides. As with *S. lineata*, this single discovery has profound implications for management and the shade from conifers and scrub is now seen as a major threat to the species. At one of the former sites scrub invasion has been cleared and nearly 800 larvae were reared and released in 1989 in an experiment to see if a colony can be established. The larval food-plant is now abundant and adults produced by the original larvae were recorded at light-traps in 1990. No adults were found when light-trapping took place in 1991 but this coincided with an extended period of adverse weather during which many species known to be resident were not recorded. Light-traps will be operated at the site again in 1992. The knowledge gained during this study indicates that this is currently a sub-optimal site. Owing to the small size of this woodland clearing and the proximity of trees and shrubs, it has been necessary to coppice the site every second winter to control the woodland regeneration and in spite of this treatment conditions at this site differ substantially from the surviving breeding grounds on heathland. The situation will not be resolved without clearance of a much larger area and use of domestic animals or other means to keep woody growth at bay.

Interest in establishing colonies of *A. caliginosa* continues, with the aim of replacing colonies that have been lost because of adverse management in the last forty years and because the species now appears to be restricted to what is basically one locality. The possibility of a return of the insect to the mainland, from which it was last seen in 1961, is being investigated by English Nature as part of their Species Recovery Plan. Meanwhile negotiations are underway to maintain and improve management at the remaining colony. Some adjacent scrub has been cleared to extend the size of the breeding grounds and further scrub clearance followed by rotational management is planned.

Pareulype berberata

The third of the Schedule 5 species, *Pareulype berberata*, was formerly widespread in Britain and reached at least as far north as Yorkshire (Waring, 1989a,b ; 1990a ; 1991c) although there is also a record from Scotland. During the late nineteenth century it was discovered that the larval food-plant, *Berberis vulgaris*, was a host of the wheat rust *Puccinia graminis* and there began an extensive campaign to eradicate *B. vulgaris* from field hedgerows and wood margins and this resulted in the loss of colonies of the moth (Barrett, 1902). There is evidence that the practice of *Berberis* destruction continues today to some extent even though modern wheat strains are resistant to the rust. Additional losses have been caused by general grubbing out of hedgerows to increase the size of fields to accommodate modern farming methods and by fires resulting from badly controlled stubble burning (Waring, 1989b ; 1991c). By the late 1970s the moth was apparently reduced to a single colony in Suffolk. This colony, which has been known since the 1860s (Waring, 1989b), has been eroded in size as bushes have been removed to accommodate improvements in nearby roads. During the 1970s the whole site was threatened with obliteration because it was in the proposed route of a new by-pass. Fortunately the eventual route taken by the by-pass narrowly avoids the site. In 1983 vandals started a fire which scorched some of the best bushes. Because of the precarious nature of this remaining colony a captive stock was established from a single female captured in May 1988. This stock has been used in three establishment trials aimed at setting up new colonies. The discovery in 1991 of larvae of a successor generation at one of the establishment sites suggests that the trial may be on the way to success. The necessity of such extreme and time-consuming measures for these species was emphasised in August 1991 when an accidental fire at the donor site burned 73% of the *Berberis* at this colony at a time when the larvae were feeding. The entire standing volume of *Berberis* before the fire was estimated to occupy only 120 m^3 (Waring, 1989b) and there is currently doubt as to whether any *P. berberata* have survived to recolonise the site if and when the *Berberis* recovers from the fire. Arrangements are underway to propagate new bushes to replace those that have been lost over the years. Meanwhile a second colony of the moth has been discovered by investigating old records of occasional adults taken at light in Gloucestershire (Waring, 1991c) and arrangements have been made to protect these breeding grounds. Surveys of a number of other sites with the potential to support colonies have been conducted (e.g. Waring, 1992a), so far without finding any more colonies. However the capture of a single adult female at light in 1990 in Hampshire suggests that at least one undiscovered colony survives so the search will continue.

Zygaena viciae and *Thetidia smaragdaria*

Two more of the Schedule 5 species are *Zygaena viciae* and *Thetidia smaragdaria*. Both of these have been covered by extensive surveys, monitoring of their single known colonies and ecological studies which are still underway.

Further details are provided by Barbour & Waring (1991) and Waring (1989c ; 1990c). The latter species has been the subject of a major captive rearing programme aimed at building up numbers of larvae for return to the wild. This has not been an easy job with this species. Whereas it was possible to produce over 1000 larvae from a few *A. caliginosa* females within one generation, *T. smaragdaria* has been much less accommodating. During 1987 only eleven larvae were found in the wild after a major survey of the Essex and Kent salt marshes to which this species has always been confined in Britain. These were used to establish a captive stock (Waring, 1989c). The females are capable of laying only 70 or 80 eggs as a rule and it has been our experience that many lay fewer or none. From eleven pre-hibernation larvae in autumn 1987 numbers have been raised in captivity to over 100 in autumn 1988 and over 600 in autumn 1989. In 1990 the captive stock was dispersed between several entomologists skilled in breeding moths and arrangements were made for releases of the progeny into the wild. However breeding success was extremely poor and resulted in just over 100 larvae only in autumn 1990. From the resulting adults over 400 larvae were reared in autumn 1991 and at least 350 have survived the 1991/92 winter. This is barely sufficient for establishment trials and many fewer than we would have expected after five years of hard work and much care. The reason for such poor reproductive success, which is a common experience among those maintaining captive moth populations, is usually attributed to inbreeding. There is no denying that the captive stock of *T. smaragdaria* is inbred. Neither of the two colonies that have been recorded in the last fifteen years have numbered more than 100 larvae at any point during this time so inbreeding has been inevitable. Another reason for the poor reproductive success could be a build up of pathogens in these small inbred populations. Larvae have been reared at low density on new potted food-plants each year and have not displayed the characteristic symptoms of viral diseases. In fact larval mortality has been very low in each generation. The poor reproductive success stems from the fact that many adults fail to pair or pair but produce few eggs or infertile ones. Arrangements are being made for specialists to examine the stock for protozoan and viral infections during 1992. One technique for reducing the possibilities of virus transmission is to surface-sterilise the eggs with a dilute solution of formaldehyde and in 1991 this was applied to a small batch of eggs to establish whether *T. smaragdaria* eggs would survive this treatment. The hatch rate was very poor in both the treated sample and a control batch from the same females. This treatment greatly increases the time that has to be spent on the culture. Protozoan infections can be controlled using drugs sprayed onto the food-plant for the larvae to ingest. Depending on the results of the examinations for pathogens, these treatments may be applied to part of the captive stock in the future.

Meanwhile the numbers of larvae found in late summer counts at the last-known wild colony in Britain have declined from 56 in 1988 to 27 in 1989, 28 in 1990 and none in 1991. The causes of loss of previous colonies have been variously attributed to land reclamation, sea-wall construction and maintenance, removal of large numbers of larvae by insect collectors, crowding of the larval food-plant, *Artemisia maritima*, by coarse grasses and trampling by domestic livestock. There is no evidence that any of these factors are responsible for the decline at the last-known colony, although a fire narrowly missed wiping out the colony in 1989. Could it be that such small colonies, reduced to fragments of their former habitat, can ultimately become too inbred or disease-laden to remain viable even if their immediate habitat remains suitable? Hence the importance of the pathogen tests.

Hadena irregularis

The latest addition to the list of moths to be given legal protection in the UK, *Hadena irregularis*, was added to Schedule 5 in 1988. The same year a major survey was organised covering all the known sites for the larval food-plant, *Silene otites*, which has been the subject of botanical surveys in recent years. The plant is confined to the East Anglian Breckland area. No larvae were found. A second survey, in 1989, covered the most promising areas again but with negative results. Subsequent enquiries indicate that the moth had almost certainly declined to extinction some years before it was proposed for inclusion on Schedule 5. The last known sighting was in 1977. This case draws attention to the need for improved and continuous monitoring of the rarest species so that the current status is always known. With only irregular surveys and out of date information species are being lost before we have time to realise and react to their decline.

Other work

While this account has concentrated on the Schedule 5 species, the breeding grounds of many other rare moths have been visited during the last five years. Surveys have been organised and assistance given in protecting and managing sites all over the UK, from the steep coastal slope inhabited by *Z. viciae argyllensis* in western Scotland to the sand-bank occupied by *Luperina nickerlii leechi* in the extreme south-west of England, the estuary on the coast of eastern England where *Gortyna borelii* resides, to the bog in west Wales where the larvae of *Eugraphe subrosea* are counted every year. The responses of moths to various types of management such as coppicing and conifer planting in ancient broad-leaved woodland, fenland management and the harvesting of wild-flower seed in hay-meadows have been examined (Waring, 1988a,b ; 1989d ; 1990d ; Waring & Haggett, 1991). A large number of independently organised moth recording and conservation projects have been promoted via publications and radio and television broadcasts and it is apparent that moths and moth conservation enjoy a higher profile now than at the inception of the project.

The future for moth conservation in the UK

Central to the development of moth conservation in the 1990s is the need to find means of sustaining a long-term programme of action. Conservation efforts remain piecemeal and sporadic, sometimes subject to the vagaries of funding but more often critically dependent on the enthusiasm and time of highly motivated local volunteers. The latter are the most valuable conservation resource. Much can be achieved simply by providing a national overview in the context of which the importance of particular local projects can be seen and attention focused. Local action groups thrive on encouragement and the realisation that what they are doing is recognised to be of value by others outside the group. There is no doubt that county-based recording will continue to thrive and that more detail will be recorded as computers and other aids make it easier to process and retrieve this information. This will be of increasing use in local conservation issues. However a national recording scheme is needed to encourage recorders to poorly worked areas and to aid the interpretation of local data. Hopefully the production of the Atlas of rarer moths will stimulate many more local projects but past experience with the Red Data Book (Shirt, 1987) suggests that this alone may be insufficient to ensure that the rarer species are conserved. Promoting recording and making recommendations for action is one thing, the logistics of ecological study and practical conservation measures can rapidly require full-time commitment to achieve even modest progress. Within the conservation organisations staff that are able to build such projects into their work programme for a few days or weeks per year and contractors and researchers wishing to tackle these jobs also find an up to date national information network useful to quickly locate other colonies or experience. This is apparent from the number of enquiries the author receives. With so much of this service now in place it is hoped that ways and means can be found to continue and build upon it in the years to come. As it is increasingly realised that moths are sensitive indicators and integrators of habitat quality and change in our environment, and as the large-scale declines of some species become more widely known, public support for the monitoring and conservation of moths will grow in the same way that it has for butterflies. The scientific value of conserving the isolated British populations for study by evolutionary biologists, ecologists and taxonomists hardly needs stating, particularly as some of the British forms are recognised as separate subspecies from those of continental Europe. One of the above species, *P. berberata*, has been collected as long series from the same site in Britain over many years, beginning in the 1860s when the colony was first discovered. In fact the great majority of specimens in British collections come from this one site. It is likely that such a wealth of preserved dried material of known origin and date will be of value to many disciplines, not just geneticists and entomologists in the future. But unless special conservation measures continue to be taken now, these populations and the link with the past will be lost. It is also true to say that for too long moth recording and conservation in Britain has proceeded with an imperfect knowledge of the situation elsewhere in Europe. The case of *S. lineata* is a good example. There must be many other cases where the biology of particular species is better known or can be more easily studied abroad, although the habits of *T. smaragdaria* indicate that the results may not always be applicable in Britain. Greater contact with workers in other European countries is desirable and Societas Europaea Lepidopterologica is the obvious medium.

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The butterfly fauna of the eastern coast of Hudson Bay and James Bay (Canada), with particular reference to the Holarctic element

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Summary

Twenty-four butterfly and three skipper species were collected at Kuujjuarapik (55° 17'N, 77° 48'W), in the forest tundra zone of northern Québec, in 1985, 1990 and 1991. This material markedly extends the known northern limit of many species, including *Clossiana bellona* (Fabricius, 1775), *Vanessa atalanta* (Linnaeus, 1758), *Incisalia polios* Cook & Watson, 1907, *Polygonia gracilis* (Grote & Robinson, 1867), *Lycaeides idas* (Linnaeus, 1761) and *Celastrina ladon* (Cramer, 1780). A massive migration of *Vanessa cardui* (Linnaeus, 1758) was observed in 1991. Certain northern species, such as *Colias nastes* Boisduval, 1832 and *Clossiana polaris* (Boisduval, 1828), are at their southern limit at Kuujjuarapik. The total fauna on the eastern coast of James Bay - central Hudson Bay, Québec (between 51° 30' and 57° 15'N; up to 100 km inland of the coast) comprises 41 species of butterflies and skippers. The proportion of circumpolar (Holarctic) species increases with the latitude. The approximate percentage of Holarctic species at James Bay sites is 50%, at Kuujjuarapik 75% and at more northern sites on Hudson Bay 90%.

Introduction

The Lepidoptera fauna of the eastern coast of Hudson Bay is rather poorly known. Thus, in the recent handbooks by Laplante (1985) and Scott (1986), the maps and other data on the distribution of butterflies in Nouveau-Québec are highly generalized. Only a few papers on the butterflies of the eastern coastal area of Hudson Bay and of James Bay have been published (Freeman, 1949 ; Laflamme & Perron, 1983 ; Gauthier & Koponen, 1987 ; Comtois & Néron, 1987 ; Layberry, 1988 ; Néron, 1990 ; Koponen, 1992). No detailed study of the butterfly fauna of any restricted locality in the Hudson Bay area is available.

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This article presents the butterfly and skipper species found by the author around the village of Kuujjuarapik (Whapmagoostui/Poste-de-la-Baleine/ Great Whale) during three summers (1985, 1990 and 1991). Data on their flying periods and habitat preferences in the area are given. The known butterfly and skipper fauna of the southeastern coasts of Hudson Bay is also discussed.

Study area, material and methods

The Kuujjuarapik area (55°17'N, 77°48'W) belongs to the southern forest tundra zone (Payette, 1983) (Fig. 1). Three conifer tree species, white spruce, black spruce and tamarack grow there at their arctic-maritime limit. Alder and dwarf birch shrubs are typical of the area. There are also small bogs and moist meadows. Open hills, barren or covered by alpine heath, are rather low, the highest summit being about 230 m. Vast alpine tundra areas are absent around Kuujjuarapik. The village is located on a sandy terrace between the Great Whale River and Hudson Bay.

Butterflies and skippers were collected and observed around the village. Lepidopterans were observed in 1985 whenever the weather permitted ; species were caught by netting, and abundant ones also recorded without catching. The study period consisted of two periods, 18th June - 8th July and 2nd August - 2nd September 1985 ; the total number of observation days was 34. In 1990 collecting was less intensive ; the main observation period was 13th July - 21st August, but some collecting was also done around mid-June. The collecting period in 1991 was short, 5th-11th July.

The author collected butterflies at Lake Ekomiak (53°23'N) 60 km south of Radisson (La Grande) in July 1990, and between Rupert River (51°30'N) and Lake Ekomiak on the James Bay Highway in July 1991. Information on collections by Layberry (1988 and unpubl.) in 1986-87 in the James Bay Highway area (between 51°30' and 53°45'N), has been included in this paper. Collections between 53°10' and 57°15'N, presented by Gauthier & Koponen (1987), are also included.

The system and nomenclature is mainly based on Laplante (1985) ; however, all subspecific and other infraspecific names have been omitted.

Results

1. *Fauna of Kuujjuarapik*

Altogether, 24 species of butterflies and three skippers were found at Kuujjuarapik (Table 1). The butterfly material included twelve Nymphalidae, five Lycaenidae, four Satyridae and three Pieridae species.

Most species were collected or observed frequently ; only *Incisalia polios* Cook & Watson, 1907 and *Speyeria atlantis* (Edwards, 1862) in 1985, *Colias nastes* Boisduval, 1832 in 1990, and *Clossiana bellona* (Fabricius, 1775), in 1991, were observed once. The species observed most often in 1985 were *Epidemia* *dorcas* (Kirby, 1837), which was seen on 20 of the total 34 observation days, and *Lycaeides idas* (Linnaeus, 1761) (18), both flying mainly in August, *Colias pelidne* Boisduval & Leconte, 1829 (14) with a very long flying period, *Oeneis taygete* Geyer, 1830 (14) and *Celastrina ladon* (Cramer, 1780) (13) flying in June-July. *Nymphalis antiopa* (Linnaeus, 1758), *Clossiana titania* (Esper, 1793), *C. selene* (Denis & Schiffermüller, 1775) and *C. frigga* (Thunberg, 1791) were also seen frequently.

Three species not found in 1985 were collected in 1990 : *Colias nastes*, and the skippers *Hesperia comma* (Linnaeus, 1758) and *Pyrgus centaureae* (Rambur, 1839) ; and one in 1991 : *Clossiana bellona*. The skippers were markedly abundant, and their absence in 1985 is presumably due to their flying pattern : only or dominantly in even years at Kuujjuarapik. The same is true for *Clossiana polaris* (Boisduval, 1828).

A massive migration of *Vanessa cardui* (Linnaeus, 1758) was observed in July 1991. More than 20 specimens were seen at Kuujjuarapik and five captured, 5th-11th July.

Moist swampy meadows were the preferred flying sites of many species at Kuujjuarapik. Species collected frequently in moist meadows and bogs were *Clossiana frigga*, *C. freija* (Thunberg, 1791), *C. titania*, *Proclossiana eunomia* (Esper, 1799), *Oeneis taygete*, *O. jutta* (Hübner, 1806), *Coenonympha inornata* Edwards, 1861, *Epidemia dorcas*, *Carterocephalus palaemon* (Pallas, 1771), *Hesperia comma* and *Pyrgus centaureae*. Species typically observed in forested sites were *Nymphalis antiopa* and *Polygonia gracilis* (Grote & Robinson, 1867), and also *Clossiana titania* and *Lycaeides idas*. Some species, such as *Vanessa atalanta* (Linnaeus, 1758), *Colias pelidne*, *Clossiana polaris*, *Agriades franklinii* (Curtis, 1798), *Oeneis taygete* and *O. melissa* (Fabricius, 1775) were often seen on open, windy hills and also on the open Hudson Bay shores. The most eurytopic species at Kuujjuarapik seemed to be *Colias pelidne*, *Pieris napi* (Linnaeus, 1758), *Clossiana selene*, *C. titania*, *Vanessa atalanta*, *Lycaeides idas*, *Celestrina ladon* and *Hesperia comma*.

2. *Fauna of the eastern coast of James Bay - Hudson Bay*

Altogether, 41 butterfly and skipper species are known from the coastal area between southern James Bay and central Hudson Bay (Table 1). This area is situated between Rupert River, 51°30'N, and Lake Minto, 57°16'N (Fig. 1). Thirteen species not caught at Kuujjuarapik in 1985, 1990 and 1991 are known from the James Bay area. *Papilio machaon* Linnaeus, 1758 and the migrating *Danaus plexippus* (Linnaeus, 1758) were mentioned by FREEMAN (1949) from the southernmost locality included, Fort Rupert (Waskaganish). The same is true for *Incisalia augustus* (Kirby, 1837), reported by LEBLANC (1985) at Rupert River. Other species, known to occur in the James Bay area (LAYBERRY, 1988 ; SCOTT, 1985), but not found by the present author include *Colias interior* Scudder, 1862, *Oeneis chryxus* (Doubleday & Hewitson, 1849), *Erebia disa* (Thunberg, 1791) and *Epidemia epixanthe* (Boisduval & Leconte, 1833).

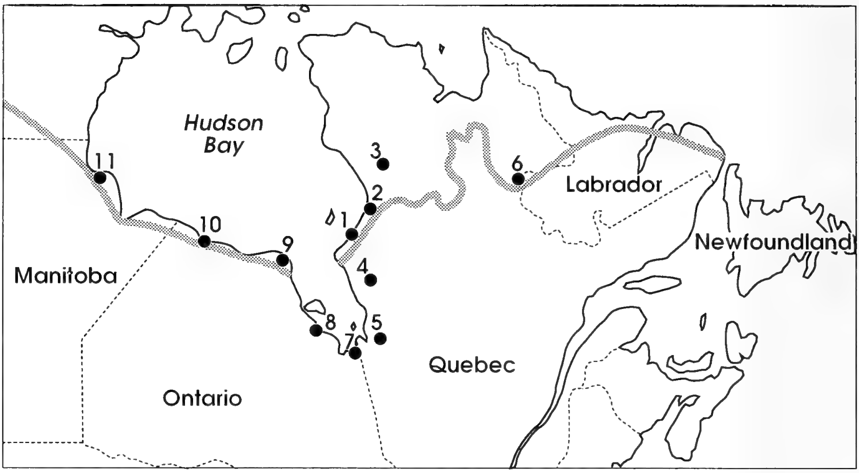

Fig. 1. Study localities in northeastern Canada. 1. Kuujjuarapik, 2. Richmond Gulf, 3. Lake Minto, 4. Lake Ekomiak, 5. Rupert River, 6. Schefferville, 7. Missisicabi River, 8. Fort Albany, 9. Cape Henriette Maria, 10. Fort Severn, 11. Churchill. Gray line indicates the northern forestline.

The author collected the skippers *Polites mystic* (Edwards, 1863), *Erynnis icelus* (Scudder & Burgess, 1870) and *Thymelicus lineola* (Ochsenheimer, 1808) at Rupert River, the southernmost study site. Of these, *T. lineola*, an introduced European species, was abundant. *Pterourus glaucus* (Linnaeus, 1758), *Phyciodes morpheus* (Fabricius, 1775) and *Basilarchia arthemis* (Drury, 1773) were caught as far north as Lake Ekomiak (53°23'N). *Vanessa cardui* occurred in great numbers along the James Bay Highway at all suitable sites in early July 1991 (see Koponen, 1992).

Of the 41 species found between Rupert River and Lake Minto, 27 have been observed by the present author at Kuujjuarapik. The number of species caught at the James Bay sites, north of Rupert River, is 32 and 19 are known from the northern forest tundra, between Richmond Gulf (17 species) and Lake Minto (Table 1).

Discussion

1. *Kuujjuarapik*

Up to now, 17 butterfly species have been reported from Kuujjuarapik (Freeman, 1949 ; Laflamme & Perron, 1983 ; Gauthier & Koponen, 1987 ; Néron, 1990). The present material includes all of these, plus the following seven butterflies which have not been found earlier at Kuujjuarapik (see Koponen, 1992) : *Colias nastes*, *Clossiana bellona*, *Speyeria atlantis*, *Vanessa atalanta*, *Polygonia gracilis*, *Incisalia polios*, and *Celastrina ladon*. The skip-

Table 1

Butterflies and skippers known from three areas on the eastern coast of James Bay - Hudson Bay (51°30′-57°15′N), based on the present material, Gauthier & Koponen (1987)[1], Layberry (1988 and unpublished)[2], Freeman (1949)[3], Comtois & Néron (1987)[4], Scott (1986)[5], and Leblanc (1985)[6]. The observation periods at Kuujjuarapik were 18th June - 8th July and 2nd August - 2nd September 1985, mid-June and 13th July - 21th August 1990, and 5th-11th July 1991. **JB** = James Bay (boreal forest zone), **KU** = Kuujjuarapik (southern forest tundra), RM = Richmond Gulf - Lake Minto (northern forest tundra)

Species	**JB**	**KU**	**RM**	**flight at Kuujjuarapik**
Papilio machaon	+[3]	-	-	-
Pterourus glaucus	+	-	-	-
Colias interior	+[2]	-	-	-
Colias pelidne	+	+	+[1]	28.6.-26.8.
Colias nastes	-	+	+[1]	04.8.
Pieris napi	+	+	+[1]	18.6.-01.8.
Clossiana selene	+	+	+[1]	30.6.-13.8.
Clossiana bellona	+	+	-	05.7.
Clossiana frigga	+	+	+[1]	23.6.-08.7.
Clossiana polaris	-	+	+[1]	22.6.-02.8.
Clossiana freija	+[1]	+	+[1]	22.6.-16.7.
Clossiana titania	+	+	+[1]	05.7.-22.8.
Proclossiana eunomia	+	+	+[1]	29.6.-06.8.
Speyeria atlantis	+	+	-	05.8.
Phyciodes morpheus	+	-	-	-
Vanessa atalanta	-	+	-	09.6.-01.7.
Vanessa cardui	+	+	-	05.7.-11.7.
Nymphalis antiopa	+	+	+[4]	18.6.-15.7.
Polygonia gracilis	-	+	-	21.6.-29.6.
Polygonia sp.	+	-	-	-
Basilarchia arthemis	+	-	-	-
Danaus plexippus	+[3]	-	-	-
Coenonympha inornata (*tullia*)	+	+	-	08.7.-05.8.
Oeneis chryxus	+[2]	-	-	-
Oeneis taygete (*bore*)	-	+	+[1]	18.6.-01.8.
Oeneis jutta	+[2]	+	+[1]	26.6.-27.7.
Oeneis melissa	-	+	+[1]	22.6.-01.8.
Oeneis polixenes	-	-	+[1]	-
Erebia disa	+[5]	-	-	-
Incisalia polios	-	+	-	21.6.
Incisalia augustus	+[6]	-	-	-
Epidemia dorcas	+	+	-	28.7.-02.9.
Epidemia epixanthe	+[2]	-	-	-
Lycaeides idas	+	+	+[1]	05.7.-02.9.
Agriades franklinii (*glandon*)	+[1]	+	+[1]	30.6.-12.8.
Celastrina ladon (*argiolus*)	+[1]	+	-	18.6.-08.7.
Polites mystic	+	-	-	-
Hesperia comma	+[2]	+	+[1]	14.7.-12.8.
Thymelicus lineola	+	-	-	-
Carterocephalus palaemon	-	+	+[1]	02.7.-08.7.
Pyrgus centaureae	-	+	+[1]	15.7.-04.8.
Erynnis icelus	+	-	-	-
Total No. of species : 41	**32**	**27**	**19**	

pers *Carterocephalus palaemon*, *Hesperia comma* and *Pyrgus centaureae* are also new to Kuujjuarapik ; however, all these skippers have been recorded north of Kuujjuarapik (Gauthier & Koponen, 1987).

According to Laplante (1985), many of the present species have a southern range in Québec, and their occurrence at Kuujjuarapik on the Hudson Bay coast is somewhat unexpected. Laplante (1985) regarded *Clossiana bellona*, *Vanessa atalanta*, *Incisalia polios*, *Speyeria atlantis* and *Carterocephalus palaemon* as species of the temperate-boreal forest zone. Gauthier & Koponen (1987) already reported *C. palaemon* from Richmond Gulf, north of Kuujjuarapik. The following species also have a southern (boreal) distribution ; their range, according to Laplante (1985), in the Québec-Labrador peninsula extends to the forest tundra area only in its maritime southeastern part on the Labrador coast (see Laplante 1985 : 218-219 ; note that Fort Rupert in his map on p. 219 should be Fort George) : *Nymphalis antiopa*, *Polygonia gracilis*, *Epidemia dorcas*, *Lycaeides idas* and *Celastrina ladon*. Of these, Néron (1990) has already reported *Nymphalis antiopa* and *Epidemia dorcas* from Kuujjuarapik. Many of the above southern species have been reported from comparable areas on the western coast of Hudson Bay in Ontario and Manitoba (Riotte, 1971 ; Klassen, 1984 ; Klassen *et al.*, 1989). Danks (1981) mentioned *Clossiana polaris*, *Colias nastes* and *Agriades franklinii* as butterfly species occurring in the Canadian High Arctic. Of the northern species, *Colias nastes*, *Clossiana polaris* and *Oeneis melissa* seem to reach the southern limit of their range around Kuujjuarapik. *Oeneis polixenes* (Fabricius, 1775) has been collected north of Kuujjuarapik (Gauthier & Koponen, 1987). Its absence from Kuujjuarapik is probably explained by the absence of large-scale tundra areas around the village.

The special flying pattern, only or predominantly in alternate years in the north (cf. Scott, 1981 ; Ferris *et al.*, 1983) can explain the uneven occurrence of some species in 1985 and 1990. Thus *Clossiana polaris* (only one specimen in 1985 and none in 1991), and *Hesperia comma* and *Pyrgus centaureae* (not found in 1985 or 1991) were markedly abundant in 1990. The opposite seemed to be true for *Clossiana freija*, *Oeneis jutta*, and *Carterocephalus palaemon*. No evidence of alternate year flight was found for the more abundant *Oeneis* species, *O. taygete* and *O. melissa* (cf. Scott, 1981 ; 1986). The data from Schefferville, central Québec-Labrador peninsula (Anthony, 1969 ; Koponen, 1980) support the even-year flying pattern of *Hesperia comma* and *Pyrgus centaureae* there as well. *Clossiana polaris* seems to be more common in even years on the Hudson Bay coast (Gauthier & Koponen, 1987 ; Néron, 1990) and near Schefferville (Anthony, 1969 ; Koponen, 1980). Due to this flying pattern, a study of butterflies in the north during one summer only may give greatly biased results.

2. *Eastern coast of James Bay - Hudson Bay*

Riotte (1971) reported 37 species from the closely comparable areas of northern Ontario : Missisicabi River - Fort Albany on James Bay and Cape

Henriette Maria - Fort Severn on Hudson Bay (51° 15′-53° N ; Fig. 1). Twenty-five of these were found on the eastern coast of James Bay - Hudson Bay, between Rupert River and Lake Minto (Soerensen's quotient of similarity ; see e.g. MAGGURRAN, 1988, QS = 0.64). KLASSEN *et al.* (1989) reported 45 species from northernmost Manitoba ; 33 of the 41 species on the eastern coast of James Bay - Hudson Bay were also mentioned for northern Manitoba (QS = 0.77). MORRIS (1980) listed 37 species of butterflies and skippers found on the Labrador coast, of these 31 were common with the present study area (QS = 0.79).

The proportion of circumpolar, Holarctic species increases with the latitude. The percentage of Holarctic species at James Bay sites is 53%, at Kuujjuarapik 74% and at more northern sites on Hudson Bay (Richmond Gulf - Lake Minto) 89%. Of the present total material, between Rupert River and the Ungava peninsula, the percentage of Holarctic species is about 60%.

The proportion of Holarctic species in the total Québec butterfly and skipper fauna is only 26% (LAPLANTE, 1985). On the island of Newfoundland this proportion is 46% and on the Labrador coast as high as 67% (MORRIS, 1980). Around Churchill, northern Manitoba on the western coast of Hudson Bay, the percentage of Holarctic species is about 57% (KLASSEN *et al.*, 1989).

The known northern limit of many species approaches the southern end of James Bay (SCOTT, 1986) and thus several species not mentioned in the present paper probably also occur in the southern James Bay area. Two northern butterflies, *Colias hecla* Lefebvre, 1836 and *C. palaeno* (Linnaeus, 1761), known from the Ungava peninsula (LAPLANTE, 1985 ; SCOTT, 1986), possibly occur in the northernmost parts of the present study area.

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Inferences about the function of genitalia in the genus *Eupithecia*, with description of a new organ (Lepidoptera, Geometridae)

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Summary

In the geometrid genus *Eupithecia*, the females usually have a sclerotized half-ring in the ductus bursae, called the colliculum. Bolte (1990) observed that this structure is lacking in the North American *E. palpata* group. In this group, the males have the 8th sternite (ventral plate) composed of two long rods and a connecting ridge. It is shown that the rods are basally articulated, and seemingly, they have a forceps-like function. In the 7th segment of the female, corresponding paired pouches for reception of the forceps' tips were found. These are named "Bolte's pockets" (crumillae boltei). A hypothesis about the interplay between the male ventral plate and the female colliculum is presented : the mainly species-specific plate is an "opener" of the colliculum, a "key". It is suggested that in *Eupithecia*, the recognition function between sexes during the early phase of copulation has shifted from the valvae to these structures. The function of the valvae is probably restricted to a stereotypic grasping at the beginning of the pairing. The later fixing, recognition and isolating functions are performed by the internal lock-and-key mechanisms formed by the aedeagus and vesica of the male and bursa copulatrix of the female, in a way similar to that published for the noctuid genus *Apamea*.

It has recently been shown that the internal genitalia of noctuid moths function as complicated lock-and-key mechanisms (Lafontaine & Mikkola, 1987 ; Mikkola, 1992). In the geometrid genus *Eupithecia* Curtis, 1825, the male vesica and the female bursa show similar structural correspondences (Mikkola, 1993). According to Petersen (1909), also in these moths, the male must deposit the spermatophore into the female bursa and appendix bursae so that its opening is against the opening of the ductus seminalis. Otherwise, the sperm transfer in the female cannot take place. Such a deposition succeeds only if the genitalia have the same specific characteristics. Thus, the internal genitalia act as isolation mechanisms.

Even though the genitalia of *Eupithecia* are shown in numerous standard works, very little is known about their function. PETERSEN (1909) is virtually the only researcher who has paid attention to the interplay of the male and female genitalia. He reached the pioneering and important concept, referred to above, that the male spermatophore must corrrespond in shape to the shape of the female bursa.

PETERSEN (1909) never made comments about the significance of the female colliculum, a structure peculiar to the genus *Eupithecia*. This is a dorsal, half-ring-formed sclerotization in the posterior part of the ductus bursae : ventrally the ductus wall is membranous (Fig. 3). Another structure which is typical of the genus *Eupithecia* is the male "ventral plate", the modified 8th sternite. Its shape is more or less species-specific, and therefore, most standard works show it for all species, even though the function of the organ was unknown.

BOLTE (1990) noted that the female colliculum is lacking in the North American *E. palpata* group, and that the ventral plate in the males of these species is composed of two long rods, fork-like. This cue inspired me to try to figure out what the relation of the ventral plate and the colliculum is ; the first results are published in this paper. A review of the lock-and-key mechanisms will be published in a separate paper in cooperation with Mr. Klaus Bolte.

Material and methods

For this study, genitalia slides made by Klaus Bolte (see BOLTE, 1990) from the Canadian National Collection, Ottawa, were used. The slides contain both the routine parts and the male vesica everted as well as the male and female abdominal skins. Most slides are stained with chlorazol black, giving a clear separation between membranous and sclerotized parts. The drawings were made using a mirror, so they correspond to the original slides.

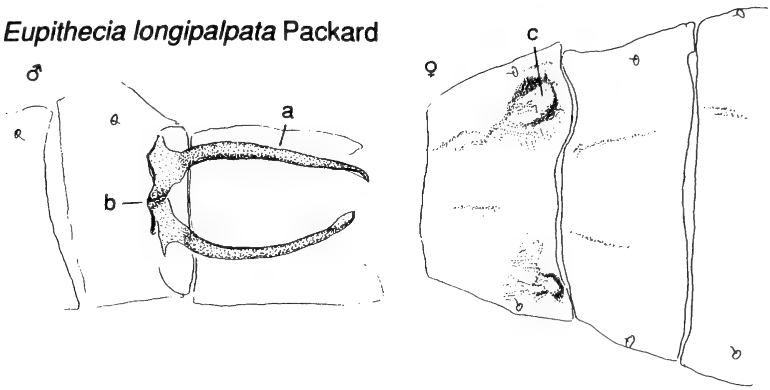
Results

According to MCDUNNOUGH (1949) the *E. palpata* group contains 22 species in North America. As BOLTE (1990) reported, the male ventral plate in the *E. palpata* group is fork-like with two more or less thin rods and with a narrow transversal ridge connecting the rods basally (Figs 1,2). In most species, like *E. longipalpata* Packard, 1876 (Fig. 1), the tips of the rods are dorso-ventrally flattened, and spatulate. The rods are usually asymmetric (noted also by MCDUNNOUGH, 1949), the left one being straighter and extending further. The stoutness and length of the rods show specific variation.

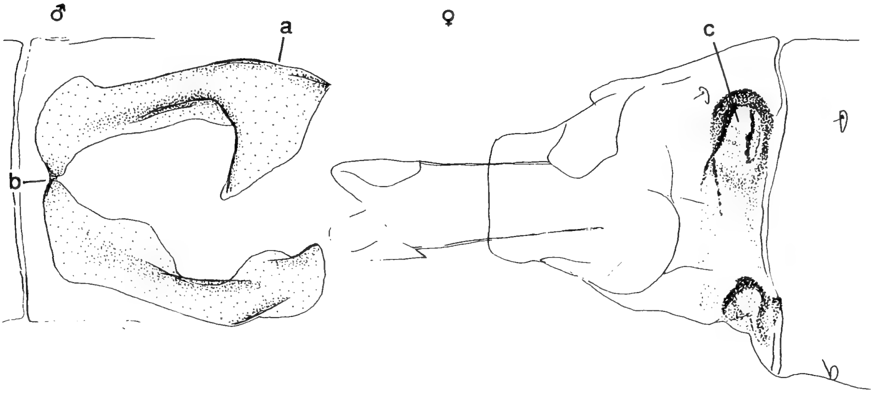
In *E. miserulata* (Grote, 1863), the plate is strongly modified (Fig. 2). The rods are strong and flat, and the tips are bent inward ; they are strongly asymmetric, the left one being much larger.

In addition to what BOLTE (1990) described, the connecting ridge is not contiguous, but there is a longitudinal crack between the lateral parts, seemingly an articulation surface, suggesting that the ventral plate could

1. *Eupithecia longipalpata* Packard



2. *Eupithecia miserulata* Grote



Figs 1, 2. Ventral views of the tips of abdomina of males (to the left, caudal direction to the right) and females (to the right, caudal direction to the left) of *Eupithecia*. The sclerotized parts are shown with heavy line and dense stippling. a = the male ventral plate (8th sternite), b = articulation of the sclerites. c = Bolte's pocket. 1) *Eupithecia longipalpata* Packard (slides CNC/GEO 5192 and 5207) ; 2) *E. miserulata* Grote (slides CNC/GEO 5659 and 5595).

function like forceps. This observation led me to search the female genitalia for the grasping points of the tips of the forceps. What was found was a pair of specialized pockets, laterally in the 7th sternite of the female skin. They are usually asymmetric (but because they are soft structures this cannot always be observed) corresponding to the male ventral plate, i.e. with the right pocket larger. The structure is described here and named **Bolte's pockets** (crumillae boltei) in honour of Klaus Bolte who published the outstanding monograph of the Canadian *Eupithecia* species (Bolte, 1990), and who observed the connection between the structure of the ventral plate and the absence/presence of a colliculum.

DESCRIPTION : Paired depressions of cuticula of female 7th sternite, anteromedial of the stigmata, near 6th/7th intersegmental membrane. Right pocket usually larger than left. Bottom of pocket scaleless, seemingly covered by sensory hairs, in *E. miserulata* bottom of pocket partly sclerotized. In fresh specimens the pockets are covered by scales of the surrounding skin. Size of pockets varies according to size of tips of ventral plate of male. Altered shape and enlarged size is found in *E. miserulata*.

Discussion

In the functional anatomy of the genitalia of species of *Eupithecia* (Geometridae) and those of the genus *Apamea* (Noctuidae) (cf. MIKKOLA 1993), the following basic differences can be observed :

1. The valvae of *Eupithecia* are soft and stereotypic, usually without specific characteristics. Those of *Apamea* are strongly sclerotized and, although they are basically quite uniform, they usually have clear specific characteristics.

2. The 8th sternite of male *Eupithecia* is a specialized, mostly species-specific structure, while the corresponding sternite in *Apamea* has an X-shaped sclerotization, similar in all species.

3. In most species of *Eupithecia*, except those of the *E. palpata* group, there is a colliculum, which is not known in the genus *Apamea*. There seems to be no doubt that the ventral plate in the *E. palpata* group acts as a tool grasping the female in her Bolte's pockets during the early phase of copulation. In Fig. 3, a hypothesis is presented to demonstrate how the ventral plate may interact with the colliculum.

The colliculum in the female's ductus bursae is a double half-ring with the dorsal side rigidly sclerotized and the ventral side membranous, laying tightly

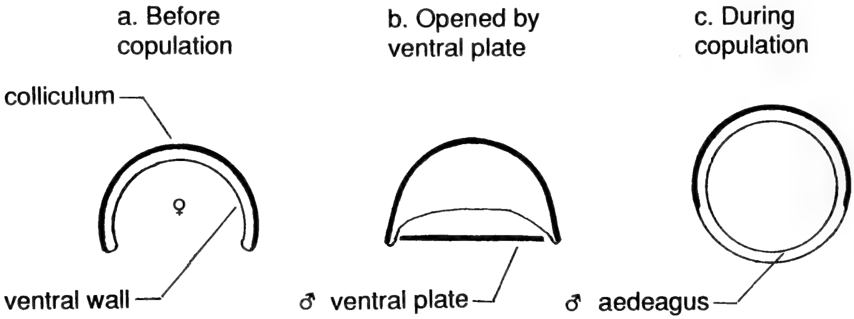


Fig. 3. Hypothetical mode of interplay between the male ventral plate and the female colliculum (transections through ductus bursae ; ventral direction downward). a : Before copulation with the ventral wall of ductus bursae against colliculum ; b : The ductus is opened by the male ventral plate ; c : When the male aedeagus is inserted into the ductus, the colliculum effectively disappears.

against the dorsal side. When *Eupithecia* bursae are inflated by injection, this point is particularly difficult to pass with a syringe needle (K. Bolte, pers. comm.) which is the same as what the male is doing with its aedeagus during copulation. The male ventral plate is usually more or less wedge-shaped. I have found some evidence concerning corresponding measurements and shapes of the ventral plate and the colliculum. Therefore, I propose that the ventral plate is a tool for the opening of the colliculum. In the early phase of copulation, it would slide ventrally of the ductus bursae, widen the distance between the lateral walls of the colliculum and thus open the ductus bursae. Once the aedeagus has gained entry to the ductus, the colliculum structure is no longer apparent. Therefore, its function must be restricted to the early phase of the copulation.

How exactly the interplay between the ventral plate and colliculum occurs, remains to be demonstrated. The former is contiguous with the abdominal scale-covered skin, and the latter is situated under the skin. It may be that the end of the abdomen is telescopic in both sexes. The colliculum of the female may well come out from the abdominal skin to be covered only by a thin inter-segmental skin. The dorsal surface of the ventral plate probably slides into the colliculum, which would require a telescopic abdomen from the male. This problem can only be solved by following and perhaps filming the early phase of the copulation.

Because the colliculum is needed only in the early phase of the copulation, the process being loosely species-specific, I propose that the valvae in the genus *Eupithecia* have lost parts of their function to the ventral plate/colliculum combination. Their function is most probably restricted to grasping the female in the first phase of copulation. In the genus *Apamea*, the valvae would have both grasping and recognition functions ; they have retained the "loosely species-specific" function. The significance of the valvae and ventral plate would be at the end, when the male has inserted the aedeagus and vesica into the ductus bursae and bursa copulatrix of the female. Thereafter, the latter structures are undertaking the fixing and sperm-transferring, and, in the case of non-conspecific copulations, isolating functions (Lafontaine & Mikkola, 1987 ; Mikkola, 1992).

Acknowledgements

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The use of wing venation as an additional aid in the identification of species of *Elachista*, as demonstrated by a study of the *E. dispunctella* (Duponchel, 1843) complex (Lepidoptera, Elachistidae)

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Summary

Many species of the genus *Elachista* present difficult identification problems. The venation is proposed as a simple identification aid within species complexes. Examples are presented from the recently published revision of the *E. dispunctella* complex, which comprises 54 species.

When *The Elachistidae (Lepidoptera) of Fennoscandia and Denmark* (TRAUGOTT-OLSEN & NIELSEN, 1977) was published, it was the first work to fully treat the northern European species of this family and as such satisfied the urgent demand for a guide to their identification. Since then, however, additional species have been described, several mistakes have been corrected and further revisions have been published.

SVENSSON (1966) published a paper on the separation of *Elachista triseriatella* Stainton, 1854 and *Elachista dispunctella* (Duponchel, 1843). As *Elachista dispunctella*, he considered specimens having genitalia with a long and slender aedeagus without cornuti ; this turned out to be a lucky choice. Svensson also mentioned that the type of *Elachista dispunctella* Duponchel in the Paris Museum was without abdomen, and thus he could not be certain about the genitalia.

In 1986, on my way to the V. SEL Congress in Budapest, I paid a visit to the late Dr. Kasy in Vienna. He generously put the museum collection of *Elachista "dispunctella"* Dup. at my disposal and gave me a free hand to study all specimens, including making venation preparations if necessary. I had already found the study of venation valuable in the 1977 work. On my way back to Spain from Budapest, passing through France I took the opportunity to visit the museum in Paris and due to the kindness of Dr. G. Luquet I was allowed to borrow the type of *Elachista dispunctella* Dup. This specimen had both forewings, but only one hindwing, and so I was able to make a venation preparation of one of the forewings.

I have since been able to study a large material of this species complex, and based largely on the venation, colour of the undersides of the wings (Duponchel stated that the undersides of the wings of *dispunctella* were white), and the male and female genitalia, a remarkably large number of new species (44) has been detected. It was found that males and females have an equal or almost equal venation and that the venation was to a high degree species specific within the complex. The results of this study have now been published in detail, including venation, male and female genitalia and colour figures of the upper and undersides of the wings (TRAUGOTT-OLSEN, 1992). The reader is referred to this paper for the characterisation of the complex.

The species could be conveniently split into 8 groups or sections, based on the venation at the apex of the cell. All of the known species are listed in Table 1, according to section, giving the countries from which they have been reported and the number of specimens examined. The venation characterising the sections are illustrated and defined in Figs 1-8. The method used for visualising the venation is given in TRAUGOTT-OLSEN & NIELSEN (1977 : 34).

Table 1

The *Elachista dispunctella* complex : List of species according to section

Species	**Distribution**	**Material examined**	
		Males	**Females**
Section I			
1. *E. hallini* Traugott-Olsen, 1992	Austria	2	
2. *E. madridensis* Traugott-Olsen, 1992	Spain	1	
3. *E. disemiella* Zeller, 1847	Spain	6	2
4. *E. mannella* Traugott-Olsen, 1992	Austria	6	1
5. *E. multipunctella* Traugott-Olsen, 1992	Austria	2	1
6. *E. skulei* Traugott-Olsen, 1992	Greece	1	
7. *E. occidentella* Traugott-Olsen, 1992	Portugal	3	
8. *E. clintoni* Traugott-Olsen, 1992	France	1	
9. *E. luqueti* Traugott-Olsen, 1992	S. France	1	
10. *E. punctella* Traugott-Olsen, 1992	Austria	1	
11. *E. catalunella* Traugott-Olsen, 1992	Spain	11	1
12. *E. cuencaensis* Traugott-Olsen, 1992	Spain	1	
13. *E. vivesi* Traugott-Olsen, 1992	Spain	8	
14. *E. vanderwolfi* Traugott-Olsen, 1992	France	4	
Section II			
15. *E. hispanica* Traugott-Olsen, 1992	Spain	3	
16. *E. minusculella* Traugott-Olsen, 1992	Turkey	1	
17. *E. blancella* Traugott-Olsen, 1992	Turkey	1	
18. *E. carascoensis* Traugott-Olsen, 1992	Italy	1	
19. *E. dispunctella* (Duponchel, 1843)	Austria	17	1
20. *E. dalmatiensis* Traugott-Olsen, 1992	S.E. Europe	19	
21. *E. bazaella* Traugott-Olsen, 1992	Spain	4	2
22. *E. veletaella* Traugott-Olsen, 1992	Spain	5	2
23. *E. maboulella* Chrétien, 1915	N. Africa	6	
24. *E. grandella* Traugott-Olsen, 1992	Austria	1	
25. *E. parvula* Parenti, 1978	Italy	4	1

Species	**Distribution**	**Material examined** **Males**	**Females**
Section III			
26. *E. cahorsensis* Traugott-Olsen, 1992	France, Germany, Ireland	7	1
27. *E. imbi* Traugott-Olsen, 1992	Austria	1	
28. *E. senecai* Traugott-Olsen, 1992	Libya	1	
29. *E. toveella* Traugott-Olsen, 1985	Spain	1	
30. *E. anitella* Traugott-Olsen, 1985	Spain	10	
31. *E. gielisi* Traugott-Olsen, 1992	France	1	
32. *E. amparoae* Traugott-Olsen, 1992	N.E. Spain	9	
33. *E. varensis* Traugott-Olsen, 1992	France	2	
Section IV			
34. *E. intrigella* Traugott-Olsen, 1992	Austria	1	
35. *E. karsholti* Traugott-Olsen, 1992	Austria	5	
36. *E. glaseri* Traugott-Olsen, 1992	S.E. Spain	1	
37. *E. moroccoensis* Traugott-Olsen, 1992	Morocco	1	
38. *E. baldizzonella* Traugott-Olsen, 1985	Spain, France	6	3
39. *E. louiseae* Traugott-Olsen, 1992	Spain	1	
40. *E. rikkeae* Traugott-Olsen, 1992	Spain	6	
41. *E. tribertiella* Traugott-Olsen, 1985	Spain	7	
42. *E. povolnyi* Traugott-Olsen, 1992	N.E. Germany, N. Austria	6	1
43. *E. pocopunctella* Traugott-Olsen, 1992	Austria, Rumania	7	1
44. *E. gerdmaritella* Traugott-Olsen, 1992	Spain	4	1
45. *E. wadielhiraensis* Traugott-Olsen, 1992	Tunisia	1	
46. *E. michelseni* Traugott-Olsen, 1992	Tunisia	2	
47. *E. bengtssoni* Traugott-Olsen, 1992	Spain	7	
48. *E. rissaniensis* Traugott-Olsen, 1992	Morocco	1	
49. *E. totanaensis* Traugott-Olsen, 1992	Spain	1	
Section V			
50. *E. berndtiella* Traugott-Olsen, 1985	France, Germany, Italy, Spain	10	
Section VI			
51. *E. contisella* Chrétien, 1922	France	1	
Section VII			
52. *E. nielspederi* Traugott-Olsen, 1992	Austria	2	
53. *E. olemartini* Traugott-Olsen, 1992	Tunisia	1	
Section VIII			
54. *E. lerauti* Traugott-Olsen, 1992	France	1	

Seventeen male specimens (plus one female) from the type locality (lower Austria) of *Elachista dispunctella* (Dup.) all had identical genitalia and white undersides to their forewings. In addition, the venation of all specimens was identical to that of the holotype. These specimens are therefore considered to be *dispunctella*. The male described and figured under that name in TRAUGOTT-OLSEN & NIELSEN (1977, Figs 94, 201, 338, 339) is the recently described *E. multipunctella* Tr.-O., whereas the female (*loc. cit.*, Figs 95, 463) was proven to be *E. pollutella* (Dup.) (TRAUGOTT-OLSEN, 1990).

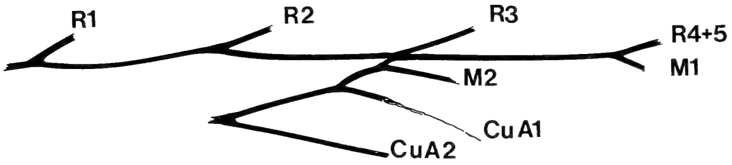


Fig. 1. Section I : R3 arising before apex of cell ; R(4+5) + M1 arising at apex of cell ; M2 arising from terminal vein, just below apex of cell.

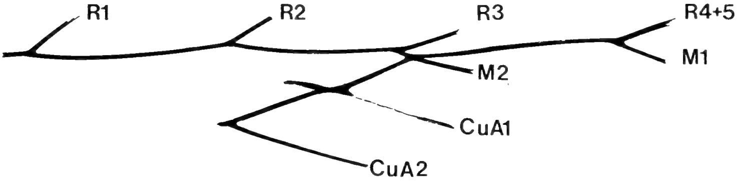


Fig. 2. Section II : R3 arising before apex of cell ; R(4+5) + M1 and M2 arising coincident at apex of cell.

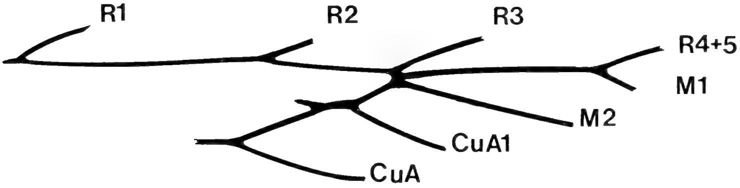


Fig. 3. Section III : R3 arising before apex of cell ; R(4+5) + M1 and M2 shortly confluent basally, arising at apex of cell.

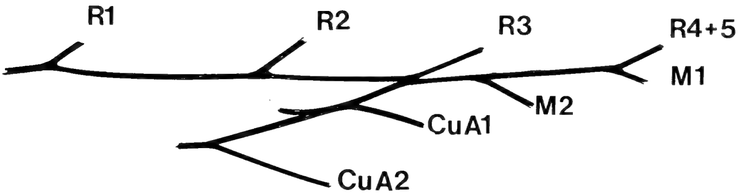


Fig. 4. Section IV : R3 arising before apex of cell ; R(4+5) + M1 and M2 confluent basally, arising at apex of cell, M2 branching off a short distance from base of R(4+5) + M1.

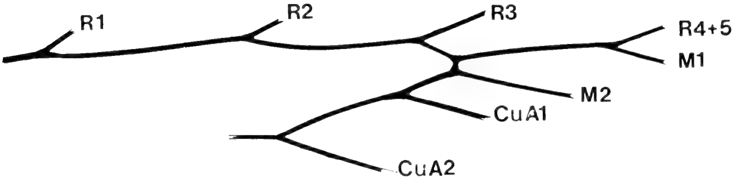


Fig. 5. Section V : R3 arising at apex of cell, coincident with R(4+5) + M1 ; M2 arising from terminal vein, just below apex of cell.

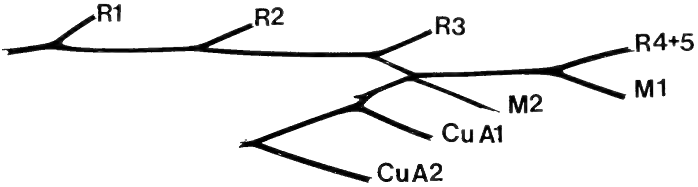


Fig. 6. Section VI : R3 arising from costal vein close to apex of cell ; R(4+5) + M1 and M2 shortly confluent basally, arising at apex of cell ; M1 arising well beyond middle of R(4+5).

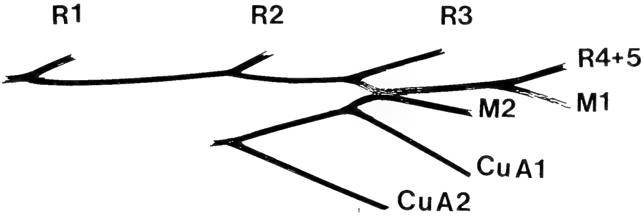


Fig. 7. Section VII : R3, R(4+5) + M1 and M2 arising coincident at apex of cell.

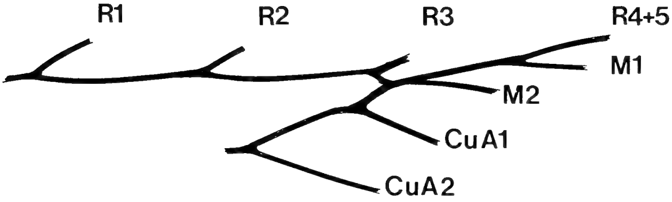


Fig. 8. Section VIII : R3 and R(4+5) + M1 + M2 arising at apex of cell ; M2 arises from R(4+5) + M1 beyond apex of cell.

Elachista mannella Tr.-O. and *E. dalmatiensis* Tr.-O. could be considered to be the species most likely to be confused with *E. dispunctella* in that they all have whitish forewing undersides. However, *E. mannella* belongs to section I, whereas *E. dispunctella* and *E. dalmatiensis* belong to section II. *E. dispunctella* has R2 arising well before the origin of CuA2, whereas *E. dalmatiensis* has R2 arising above the origin of CuA2. Additional differences between these three species can be found in details of the genitalia : Vinculum, juxta lobe, digitate process, anellus and aedeagus (Fig. 9).

To further illustrate the species specific venation, the venation, vinculum and uncus of four species belonging to section IV are compared in Fig. 10. *E. intrigella* has R2 arising well before the base of CuA2, while in *E. karsholti* R2 arises beyond the base of CuA2, paralleling the specific differences in the vinculum. The size of the anellus sac, wing pattern and antennal characters also distinguish the species (Traugott-Olsen, 1992). In *E. baldizzonella*, the saccus is rather pointed, while that of *E. tribertiella* is rounded. In *E. baldizzonella* the distance between the base of R3 and the apex of the cell is much longer than in *E. tribertiella*. R2 arises well before or well after the base of CuA2 in *E. baldizzonella* and *E. tribertiella* respectively. With these characters, it should be easy to distinguish these species. An additional character is seen in the uncus lobes, which are narrowly incised in *E. baldizzonella* and broadly incised in *E. tribertiella*.

Discussion

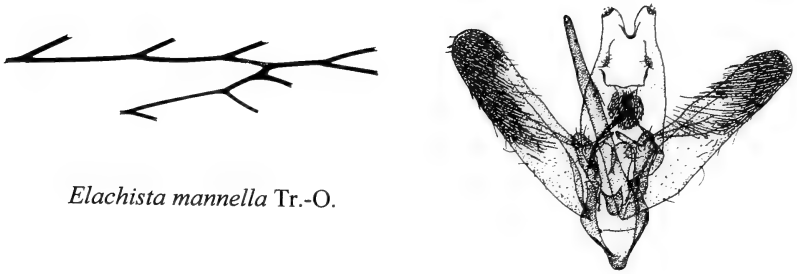
Colleagues have often been confused when I have tried to explain my points of view on the value of the venation in species identification. I will try to clarify a few points.

1. The results presented here concern only the *Elachista dispunctella* complex. Similar and parallel situations have been found in the *Elachista triseriatella* and *Elachista dispilella* complexes.

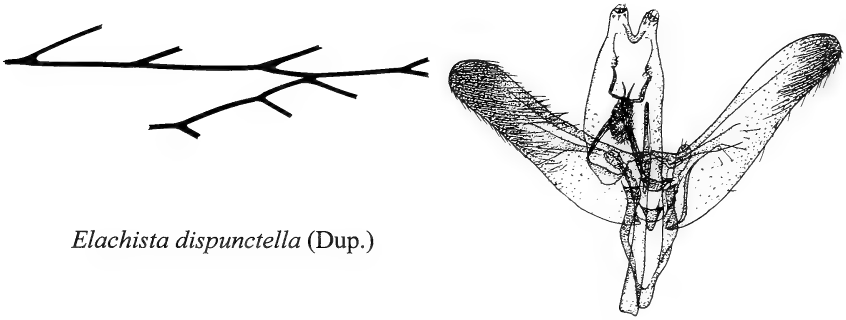
2. A complex is first established by the common characters of the genitalia in both sexes and not necessarily including the study of the venation. In two different complexes I have found equality in the specific venation, demonstrating that the venation alone cannot be used to identify a species without knowing to which complex it belongs. The genitalia remain the single most important character to separate species and species complexes, although other factors such as wing markings biology must also be taken into account. The venation is only a separating character for the species within the complex and can be used to group the species.

3. Any description of a new elachistid species will have to state the complex to which the new species belongs, with diagnoses and discussion of all the species of the complex and full descriptions of the adults, including genitalia and venation.

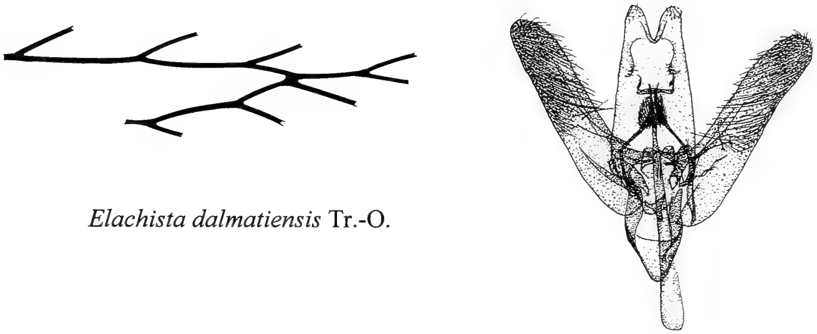
4. Venation is only a secondary character emphasising the polyphyletic nature of the genus *Elachista*. To arrive at a proper division of this conglomerate



Elachista mannella Tr.-O.



Elachista dispunctella (Dup.)



Elachista dalmatiensis Tr.-O.

Fig. 9. Forewing venation (apical part) and male genitalia of *Elachista dispunctella* (Dup.), *E. mannella* Tr.-O. and *E. dalmatiensis* Tr.-O.

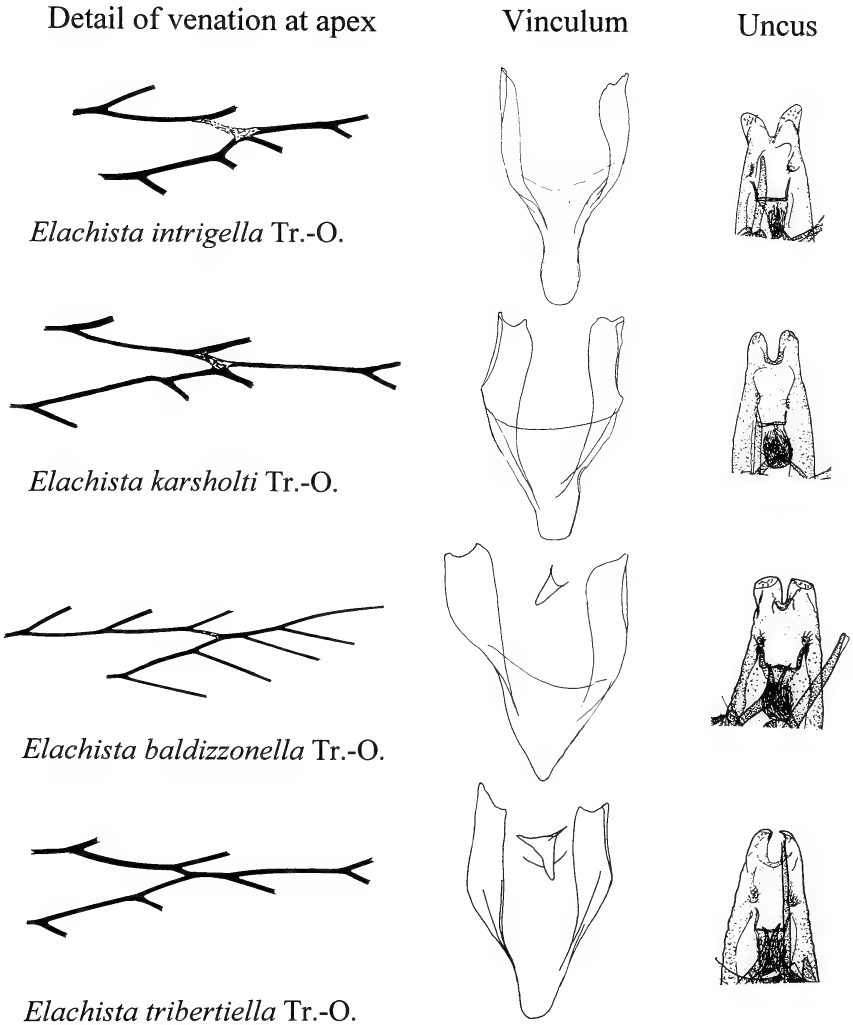


Fig. 10. Forewing venation, vinculum and uncus of four representative species of section IV of the *Elachista dispunctella* complex. Not drawn to scale.

it will be necessary to split the genus into many monophyletic units, such as the complexes mentioned here, which can be understood as a further division of the groups presented in TRAUGOTT-OLSEN & NIELSEN (1977).

It is not suggested that the evolutionary relationships between species within a complex can be determined from their venation, rather that the intra-specific variation is rather small and the inter-specific variation rather large, thereby allowing this character to be used in combination with other characters as an aid to identification. It has also helped to refer previously unknown female specimens to their male counterparts, and vice versa. An advantage of using the venation as an identification aid is that preparations are less likely to suffer the distortions often found in genitalia preparations, thereby avoiding errors of interpretation.

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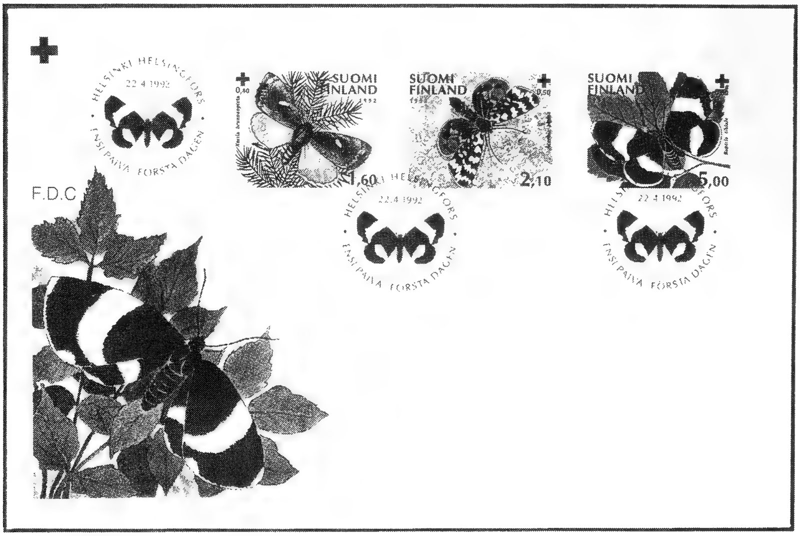
TRAUGOTT-OLSEN, E. & NIELSEN, E. S., 1977. The Elachistidae (Lepidoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 6. 299 pp. Klampenborg, Denmark.

The ladies enjoyed visiting the many attractions of Helsinki.



The Finnish Post Office issued these stamps and cover during the Congress. The stamps depict *Xestia brunneopicta* (Matsumura, 1925), *Acerbia alpina* (Quensel, 1802) and *Baptria tibiale* (Esper, 1790), the Congress emblem (60% actual size).

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The genitalia of *Eudasychira* Möschler ; morphology and evolution (Lepidoptera, Lymantriidae)

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Summary

A revision of the genus *Eudasychira* Möschler was undertaken in 1983. At that time it was noted that the male genitalia offer many good diagnostic features at the species level. The evolutionary significance of the complex structure of the male genitalia has now been investigated. The studied characters have been interactively analysed with the HENNIG program. The resulting 17 trees showed that there were not too many discrepancies between the characters, but a well-marked infrageneric classification could not be proposed. The problems in the nomenclature of the different parts of the male genitalia are explained and a few data concerning the distribution of the species is also mentioned.

The male genitalia of the taxa recognized as belonging to the genus *Eudasychira* are very complex (Dall'Asta, 1983). Thorough examination showed that these genitalia possess a unique feature within the Lymantriidae : a peculiar form and position of the saccus. Instead of being a tubular structure extending midventrally below the valvae, the saccus extends above the valvae. This is most easily seen in *E. quinquepunctata* (Fig. 1), the type species of the genus, where the valvae join ventrally and their ventral edges bend dorsally back cephalad forming the subrectangular saccus on which the penis can slide. Describing this character in another way, it can be said that the attachment point of the valvae to the saccus is situated below instead of above, and that consequently the saccus is suspended between these valvae. This peculiar feature of the saccus transforms quite a few other parts of the genitalia and the transformations of the valvae themselves are the most striking. Instead of being flattened sacs, they are semi-circularly bent in order to leave space medially for the saccus. This peculiar form of saccus and valvae can be considered a unique apomorphic character to distinguish taxa belonging to the genus *Eudasychira* from all other Lymantriidae.

Examining all preparations of Lymantriidae available proved that this genus only occurs in the Afrotropical region. In some species the saccus situated

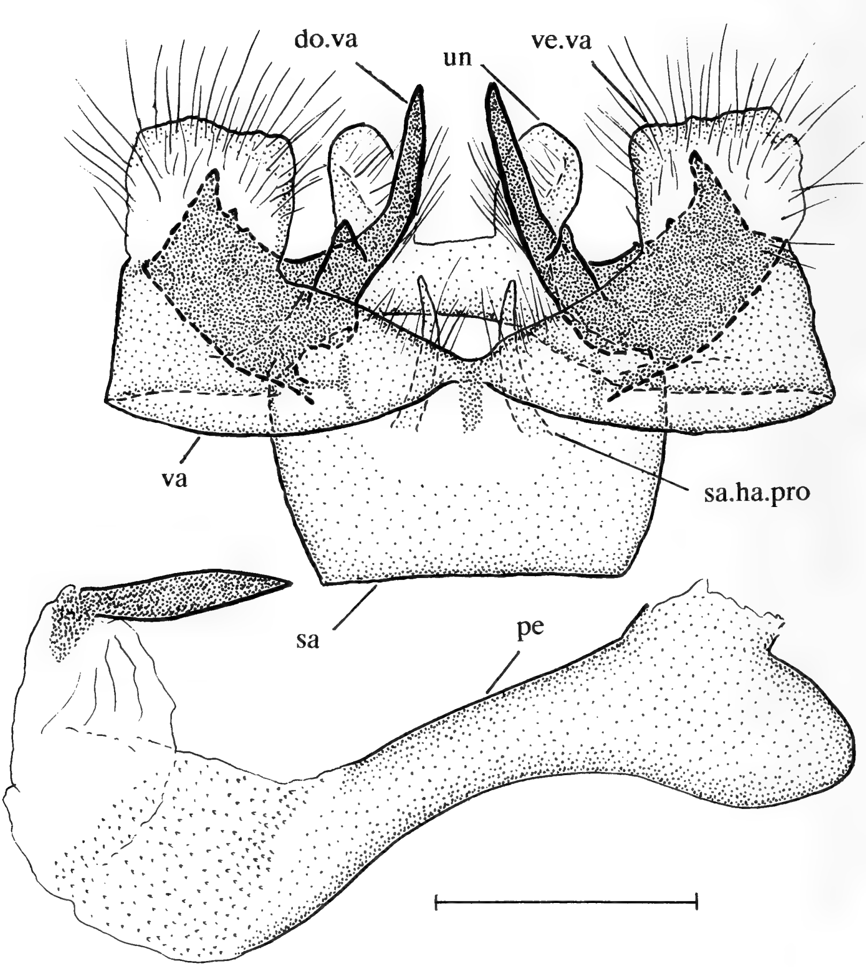

Fig. 1. Male genitalia of *Eudasychira quinquepunctata* Möschler. do.va. : dorsal portion of valva ; pe : penis ; sa : saccus ; sa.ha.pro : saccus hairy process ; un : uncus ; va : valva ; ve.va : ventral portion of valva. Scale : 1 mm.

above the ventral portion of the valvae can be rather small ; the valvae are then attached to its lateral edges and remain flattened. Including the species with these flattened valvae, a total of 33 species can now be recognized in the genus *Eudasychira*.

The unique forms of saccus and valvae are not the only peculiarities of the genus. The male genitalia of the taxa of the genus *Eudasychira* possess at least three other distinct structures not present in any other Lymantriidae, and for which no nomenclature exists in the literature on the morphology of male genitalia of Lepidoptera in general. One of these are the two hairy processes within the saccus (Fig. 1, sa.ha.pro). These hairy processess occur also in other species where they are situated on the edge of the rim saccus-valvae ; in this case these hairy processes are protruding outside the genitalia instead of being situated within the saccus. In some species, more sclerotized processess can occur in the same place as where the hairy processess of *E. quinquepunctata* are situated. Due to the fact that they are more sclerotized, never hairy and always situated at the same position, they cannot be considered homologous to the hairy processes, which are always elongate. These sclerotized processes on the other hand can display quite different forms (characteristic for the species) and can even transform into paired hooks protruding outside the genitalia from within the saccus. These two kinds of processes occur only in species with circularly bent valvae, as in *E. quinquepunctata*. In some species with flattened valvae on the other hand (and also in a species with forceps-like valvae) a long ventral ribbon (having at least the length of half of the genitalia) can be attached to the distal portion of the saccus. This ribbon can be simple or divided and is also a character unique within the Lymantriidae.

Apart from these characters, some species of *Eudasychira* display other peculiar structures characteristic of a limited number of its species. Some of these characters can only be considered transformations of parts of the valvae or other 'recognisable' parts of 'classic' types of genitalia (uncus, vinculum, etc.). But it should be borne in mind that the male genitalia of species of *Eudasychira* can be of very different forms and that sometimes single species can display some peculiar processes or forms of valvae unique within the Lymantriidae.

The above findings once again raise the question of the use of a "nomenclature of convenience" for naming the different parts of the genitalia in Lepidoptera (Klots, 1970 : 116). If distinct names have to be given to all new structures of the genitalia, in the genus *Eudasychira* alone this would mean the introduction of at least three new names. Therefore, together with the pertinent remarks of Sibatani (1972) on Klots' paper the nomenclature and glossaries of terms to be used in describing male genitalia of Lepidoptera should be considered established by those two papers. One should avoid proposing new names as Weller (1990) has done for a group of nystaleine Notodontidae.

To gain some insight into the evolutionary trends of the different characters within the species, all characters of all species have been coded and this data analysed with the HENNIG 86 program. The resulting 17 trees showed that there were not too many discrepancies between the characters, but a well-marked infrageneric classification could not be proposed. Many of the taxa were isolated, or in pairs, sister groups of the rest of the tree (a kind of chaining), but in all trees the species with flattened valvae are situated near the root of the tree and the species group with the large saccus and the bent valvae always clusters at the end. This could show a trend, i.e. saccus becoming larger when more apomorphic characters are present, which was also subjectively felt at the moment of coding.

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Genotypic variability in western European members of the *Erebia tyndarus* species group (Lepidoptera, Satyridae)

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Summary

Relationships between West European species of the *Erebia tyndarus* group have been investigated by means of enzyme electrophoresis. Within *E. cassioides* s.l. two genetically distinct groups of populations exist, one occurring in the eastern Alps (*E. cassioides* s.str.) and another in the western Alps, the Italian Apennines and the Pyrenees (E. (*cassioides*) *carmenta* Fruhstorfer, 1909). In order to ensure nomenclatural stability, a neotype has been designated for *Papilio cassiodes* Reiner & Hohenwarth, 1792.

Zusammenfassung

Die Beziehungen zwischen West-europäischen Arten der *Erebia tyndarus* Gruppe wurden mit der Hilfe elektrophoretischer Methode untersucht. Bei der *E. cassioides* s.l. kann man zwei genetisch verschiedene Populationengruppen unterscheiden : eine in den Ost-Alpen (*E. cassioides* s.str.) und die andere in den West-Alpen, in den italienischen Apenninen und in den Pyrenäen (*E.* (*cassioides*) *carmenta* Fruhstorfer, 1909). Um eine nomenklatorische Stabilität zu erreichen, wurde für *Papilio cassioides* Reiner & Hohenwarth, 1792 ein Neotyp gewählt.

Résumé

Les relations phylétiques entre les espèces ouest-européennes du groupe de *Erebia tyndarus* ont été étudiées au moyen de l'analyse électrophorétique des enzymes. Deux groupes de populations génétiquement distinctes ont été décelées au sein d'*E. cassioides* s.l., l'une vivant dans les Alpes orientales (*E. cassioides* s.str.) et l'autre comprenant les populations des Alpes occidentales, des Apennins italiens et des Pyrénées (*E.* (*cassioides*) *carmenta* Fruhstorfer, 1909). Dans l'intérêt de la stabilité de la nomenclature, un néotype de *Papilio cassiodes* Reiner & Hohenwarth, 1792 a été désigné.

Introduction

Warren (1936) originally classified the *Erebia tyndarus* species complex within a broader *E. pluto* group. It was considered to include *E. tyndarus* (Esper, 1781), *E. ottomana* Herrich-Schäffer, 1847 and *E. callias* Edwards, 1871, each subdivided into many subspecies. A number of later authors contributed to raising to species rank one or another of these subspecies, whereas meanwhile a few totally new species have been described. Currently, also *E. cassioides* (Reiner & Hohenwarth, 1792), *E. hispania* Butler, 1868, *E. iranica* Grum-Grshimailo, 1895, *E. dromulus* Staudinger, 1901, *E. calcarius* Lorković, 1953 and *E. nivalis* Lorković & de Lesse, 1954 are considered distinct species by most authors, so bringing the total of members of the *E. tyndarus* group to nine.

As male and female genitalia are very similar throughout the group (de Lesse, 1960) and as a consequence of the fact that these species are rarely found in cohabitation, Niculescu (1985) reverted to the original suggestion of Warren that they should all be considered separate subspecies within a polytypic complex. In at least one case, however, cohabitation does occur : *E.* (*iranica*) *transcaucasica* and *E. ottomana* are known to fly together in E. Turkey. Members of the *E. tyndarus* group are characterized by their small size, rounded wing shape, the presence of a normally reduced orange-brown stripe on the apical third of the wings, surrounding a pair of small black spots, pupillated white. The hind wings are normally ash-grey on the ventral surface, often with a yellowish tinge in the females. Males lack androconial scales. In the male genitalia, the valva shows a series of upwards and rearwards directed spines, the most proximal of which is normally the largest. The rear half of the valva itself recalls that of *E. pluto* (Warren, 1936), as it tapers caudad rather smoothly, without any real interruption between what this author called a 'shoulder', a 'neck' and a 'head'. Caterpillars appear finely pubescent due to the presence of many short setae. All taxa of this group are alpine or subalpine, perhaps with the exception of *E. ottomana*, which can often colonize the upper parts of the montane vegetational level. All are Palaearctic, but the range of *E. callias* extends to the Nearctic.

The karyological study of this group, carried out by Lorković (1941) and de Lesse (1960), demonstrated that haploid chromosome complements vary between species. *E. tyndarus* and *E. cassioides* have n = 10 ; *E. calcarius* n = 8 ; *E. nivalis* n = 11 ; *E. callias* n = 15 ; *E. hispania hispania* n = 25 ; *E. hispania rondoui* n = 24 ; *E. ottomana* n = 40 ; *E. iranica iranica* and *E. iranica savalanica* n = 51 ; *E.* (*iranica*) *transcaucasica* n = 52, *E. dromulus* n = 51 or 52.

Warren (1955, 1981) taking again in consideration the taxonomy of this group, came to rather different conclusions. This author, in fact, doubted that *E. cassioides*, first described from the Großglockner (Austria), really inhabits this region. As a consequence of the fact that Reiner & Hohenwarths' figure, later designated as lectotype of *E. cassioides* (Lorković & de Lesse,

1955) cannot be identified with any known species, he considered *E. cassioides* a nomen nudum, perhaps to be identified with *E. nivalis*, a species also described from the Großglockner. He also split what was formerly known as *E. cassioides* into two species, namely *E. neleus* (Freyer, 1833) and *E. aquitania* Fruhstorfer, 1909, on the basis of some subtle morphological characters of the wing shape (more pointed in *E. neleus*). Among more recent authors, however, only von Mentzer (1960) followed this suggestion ; most other authors (de Lesse, 1956 ; Higgins, 1975, etc.) maintained *E. cassioides* as a valid and single species.

The present work deals with the West European members of the *Erebia tyndarus* species group and aims at the clarification of some of the taxonomic problems outlined above, by the study of electromorph variation. Only *E. cassioides arvernensis* Oberthür, 1908, from the Mont Dore (Auvergne, France) and *E. cassioides dolomitensis* Goltz, 1930 from the Italian Dolomites and Caravanche Alps remain, for the moment, unstudied.

Materials and methods

Preparation of samples

Twenty-four populations of the *E. tyndarus* species group were scored for electromorph variability, for a total 290 specimens. Collection data for each of these populations are listed in Tab. 1, where, as regards western populations of *E. cassioides*, Warren's (1955, 1981) suggestion that *E. neleus* and *E. aquitania* may represent separate species was followed, for the sake of clarity. One population of *E. gorge* from Colle del Dragone (Province of Potenza, S.Italy) was included as an outgroup.

The wings were immediately removed on collection with sharp scissors and the whole bodies were frozen in liquid nitrogen while still alive. The specimens were stored in the same medium. Samples were prepared for electrophoresis as follows. Individual butterfly bodies were thawed in 250 µl of an ice-cold homogenizing solution (NADP 0.125 mM, 2-mercaptoethanol 1.14 mM ; pH range between 6-8) and macerated with an electric tissue grinder. Centrifugation at 13,000 x g for 15 minutes permitted the separation of a clear supernatant. Care was taken to avoid overheating during both homogenization and centrifugation. Homogenates were stored at –80° C in 5-15 µl aliquots in microtubes.

Electrophoresis

Electrophoresis was carried out on Cellogel sheets at 4° C. Buffer systems and staining techniques were similar to those described by Meera Khan (1971) and Richardson *et al.* (1986). Thirteen gene-enzyme systems were studied for a total of 17 loci. Genetically interpretable banding patterns could be obtained for : glycerol-3-phosphate dehydrogenase (E.C.1.1.1.8) (αGPD), malate dehydrogenases (E.C.1.1.1.37) (MDh-1, 2), isocitrate dehydrogenases (E.C.1.1.1.42) (IDh-1, 2), 6-phosphogluconate dehydrogenase (E.C.1.1.1.44) (6PGD), glucose-6-phosphate dehydrogenase (E.C.1.1.1.49) (G6PD), glutam-

Table 1

Populations of the *Erebia tyndarus* group sampled. Western populations of *E. cassioides* are classified according to Warren

Locality	Country, Region	No.	Symbol
Coll. de las Sabinas	Spain, Sierra Nevada, Granada	10	H1 (*hispania hispania*)
P.to de San Glorio	Spain, Cantabrian M.tns, Cantabria	10	N1 (*neleus*)
Emb. de Urdiceto	Spain, Pyrenees, Huesca	13	H2 (*hispania rondoui*)
P.to de Envalira	Andorra, Pyrenees	14	N2 (*neleus*)
Mont Canigou	France, Pyrenees, Pyr. Or.	16	H3 (*hispania rondoui* f. *goya*)
Le Tanargue	France, M. Vivarais, Ardèche	9	O1 (*ottomana tardenota*)
C.le dell'Agnello	Italy, Cottian Alps, Piedmont	14	A1 (*aquitania*)
Val Veny	Italy, Graian Alps, Val d'Aosta	11	A2 (*aquitania*)
P.so Gran S. Bernardo	Italy, Pennine Alps, Val d'Aosta	14	Ty (*tyndarus*)
Alpe Pozze, m 1800	Italy, Alpi Retiche, Trentino	12	C1 (*cassioides*)
Alpe Pozze, m 2000	Italy, Alpi Retiche, Trentino	14	C2 (*cassioides*)
Alpe Pozze, m 2300	Italy, Alpi Retiche, Trentino	12	C3 (*cassioides*)
Val Nambrone	Italy, Alpi Retiche, Trentino	10	C4 (*cassioides*)
Zirknitztal	Austria, Hohe Tauern, Carintia	13	C5 (*cassioides*)
Hochtor	Austria, Hohe Tauern, Carintia	6	Ni (*nivalis*)
M. Altissimo di Nago	Italy, Baldo M.nt, Trentino	13	O2 (*ottomana benacensis*)
M. Cavallo	Italy, Prealpi Carniche, Friuli	12	Ca (*calcarius*)
P.so di Pradarena	Italy, Appennino Tosco-Emiliano, Emilia	8	A3 (*aquitania*)
M. Cimone	Italy, Appennino Tosco-Emiliano, Emilia	14	A4 (*aquitania*)
F.lla del Fargno	Italy, Appennino Marchigiano, Marche	16	N3 (*neleus*)
M. Cristo	Italy, Appennino Abruzzese, Abruzzi	13	N4 (*neleus*)
Val. Capo la Serra	Italy, Appennino Abruzzese, Abruzzi	12	N5 (*neleus*)
Majella	Italy, Appennino Abruzzese, Abruzzi	12	N6 (*neleus*)
Colle del Dragone	Italy, Pollino, Lucania	12	N7 (*neleus*)
Colle del Dragone	Italy, Pollino, Lucania	1	Go (*gorge*)

ate-oxaloacetate transaminases (E.C.2.6.1.1) (GOT-1, 2), glutamate-pyruvate transaminase (E.C.2.6.1.2) (GPT), hexokinase (E.C.2.7.1.1) (HK), pyruvate kinases (E.C.2.7.1.40) (PK-1, 2), phosphoglucomutase (E.C.2.7.5.1) (PGM), mannosephosphate isomerase (E.C.5.3.1.8) (MPI), phosphoglucose isomerase (E.C.5.3.1.9) (PGI), esterase (E.C.3.1.1.1) (Es). Isozymes and alleles were designed numerically according to their decreasing mobility rate.

Statistical analyses

Several genetic distance indexes were calculated (Cavalli-Sforza and Edward arc and chord distances, 1967 ; Rogers **D**, 1972 ; Wright's modification of Rogers **D**, 1978 ; Nei's **D**, 1972 ; Hillis modification of Nei'S **D**, 1984). Dendrograms using UPGMA method of SOKAL & SNEATH (1963) and FITCH & MARGOLIASH method (1967) were constructed from these distances. A phylogenetic tree connecting all populations studied was obtained by the "Continuous Characters Maximum Likelihood Method" (CONTML ; FELSENSTEIN, 1981, 1985). This program assumes that each locus evolves by genetic drift, so that gene frequencies may be considered to behave like particles undergoing pure Brownian-motion.

Results

Allele frequencies are shown in Table 2. The overall number of alleles detected at 17 loci of all *Erebia tyndarus* species group studied amounts to 64 (mean per locus 3.76, range 2-8). No locus proved monomorphic across the whole sample. An additional private allele (HK 110) was identified in *E. gorge*.

The allele GOT-1 90 was found in the three populations of *E. hispania* only ; the allele GOT-1 110 is diagnostic for *E. nivalis*, PK-1 115 for *E. ottomana*. Studied populations of *E. tyndarus*, *E. neleus* (7), *E. aquitania* (4). *E. cassioides* (5), and *E. calcarius* (1) did not show any private allele.

All dendrograms obtained by the various distance and clustering methods outlined above concur to a single picture :

1. *E. gorge* (outgroup), as expected, proved to be the most genetically different taxon (**D** = 0.719). The *E. tyndarus* group, accordingly, may represent a monophyletic unit. Its first split occurs at Nei's **D** = 0.407.

2. Populations of *E. cassioides* (*E. neleus* + *E. aquitania*) from the Italian Apennines, the western Alps, the Pyrenees, the Cantabrian Mountains (western populations of *E. cassioides*, 11 populations) cluster together at much lower values (Nei's **D** = 0.015).

3. Populations of *E. cassioides* from the central-eastern Alps (eastern *E. cassioides*, 5 populations studied) also cluster together at low distance (Nei's **D** = 0.016).

4. Eastern and western *E. cassioides*, in contrast, cluster with each other at a considerably higher level of distance (Nei's **D** = 0.071).

Table 2

Allele Frequencies at 17 shared non-monomorphic loci in 25 populations. Populations are numbered as in Table 1.
For some enzyme not all individuals of all populations were scored. '-' indicates that in the population scoring was not possible

		A1	A2	A3	A4	N3	N4	N5	N6	N7	N1	N2	C1	C2	C3	C4	C5	Ca	Ty	O2	O1	Ni	H1	H2	H3	Go
αGPD	110																								0.04	
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00
MDH-1	110					0.03								0.04					0.04						0.04	
	100	1.00	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.92	0.96	0.95	1.00	1.00	0.96	1.00	1.00	0.67	1.00	1.00	0.96	
	95													0.04								0.33				
	80														0.04	0.05										1.00
MDH-2	170															0.05										
	150		0.05																		0.06					
	100	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.94	1.00	1.00	1.00	1.00	1.00
IDH-1	110		0.06									0.17		0.05												-
	100	0.91	0.89	0.60	0.92	1.00	1.00	1.00	0.89	1.00	0.93	0.72	0.96	0.86	0.92	0.70	0.94		1.00	1.00	0.31		0.95	1.00	1.00	-
	90	0.09	0.06	0.40	0.08				0.11				0.04	0.09	0.08	0.30	0.06	1.00			0.69	0.92				-
	70										0.07	0.11											0.05			-
	65																					0.08				-
IDH-2	125		0.14																							
	120																						0.10			
	100	1.00	0.86	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00
6PGD	140										0.06	0.09				0.17	0.27									
	130										0.17	0.09	1.00	1.00	1.00	0.83	0.73			0.23	1.00	0.42				
	100	0.92	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.78	0.82						1.00	1.00	0.77		0.58	1.00	1.00	1.00	1.00
	90	0.08																								
G6PD	130																						0.33			
	120											0.08					0.04						0.67	1.00	1.00	1.00
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.92	1.00	1.00	1.00	1.00	0.96	1.00	1.00	1.00	1.00	1.00				
GOT-1	120									0.10								0.17	0.08							1.00
	115																			0.50	1.00					
	110																					1.00				
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.83	0.92	0.50						
	90																						1.00	1.00	1.00	
	80													0.05												

		A1	A2	A3	A4	N3	N4	N5	N6	N7	N1	N2	C1	C2	C3	C4	C5	Ca	Ty	O2	O1	Ni	H1	H2	H3	Go
GOT-2	160		-														-			-		-	0.56	-	-	-
	100	1.00	-	1.00	0.94	1.00	0.93	1.00	1.00	0.86	1.00	1.00	1.00	1.00	1.00	1.00	-	1.00	1.00	-	1.00	-	0.44	-	-	-
	50	-			0.06		0.07			0.14							-			-		-		-	-	-
GPT	100	1.00	-	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	-	1.00	-	-	-	1.00	1.00	-	-	-	0.22	-	-	1.00
	60		-										-		-	-	-			-	-	-	0.33	-	-	
	40		-										-		-	-	-			-	-	-	0.44	-	-	
HK	110																									1.00
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.62	1.00	1.00	1.00	1.00	1.00	1.00	1.00	
	90																	0.37								
PK-1	115																			1.00	1.00					-
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00			1.00	1.00	1.00	1.00	-
PK-2	110																						1.00	0.08		
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00		0.92	1.00	1.00
PGM	135								0.04							0.05										
	125											0.09											0.35			
	110		0.30	0.37		0.22	0.25		0.43	0.41					0.36		0.05								0.04	
	100	0.95	0.65	0.62	1.00	0.66	0.75	1.00	0.54	0.59	1.00	0.91	1.00	1.00	0.45	0.95	0.70	1.00	1.00	1.00	1.00	1.00	0.65	1.00	0.96	
	90		0.05			0.12									0.18		0.25									
	80	0.05																								1.00
MPI	120	0.09							0.08		0.07	0.05														-
	100	0.86	1.00	1.00	1.00	1.00	1.00	1.00	0.92	1.00	0.86	0.95	1.00	1.00	1.00	1.00	1.00	1.00		1.00	1.00					-
	80	0.05									0.07											1.00				-
	75																						1.00	0.96	0.50	-
	70																		1.00					0.04	0.50	-
PGI	140										0.10															
	135																		0.04					0.04		
	110	0.08	0.10			0.30	0.15		0.36		0.10	0.08	0.04		0.12	0.10	0.05		0.71					0.08	0.10	0.50
	100	0.79	0.90	0.94	0.83	0.70	0.80	0.83	0.61	0.91	0.45	0.67	0.96	0.96	0.87	0.90	0.95	1.00		1.00	1.00	1.00	0.35	0.88	0.90	
	90																						0.60			
	85	0.12		0.06	0.17		0.05	0.17	0.04	0.09	0.30	0.21		0.04					0.25							0.50
	65										0.05	0.04														
	40																						0.05			
ES	120																			1.00		0.17	1.00	1.00	0.07	-
	110																	0.05	0.33		1.00	0.83			0.50	-
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	0.67						0.43	-

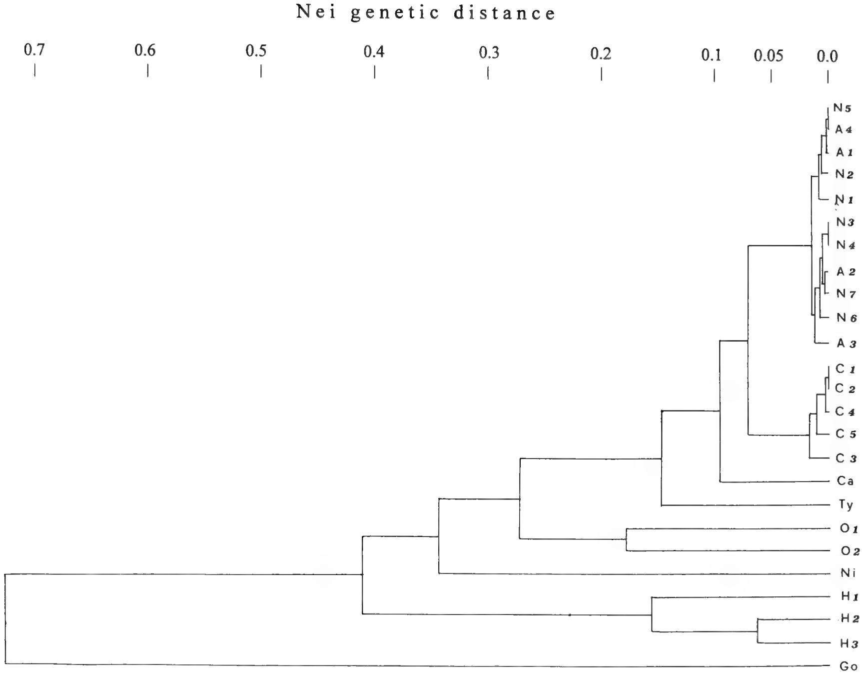

Figure 1. Dendrogram based on Nei's Distances.

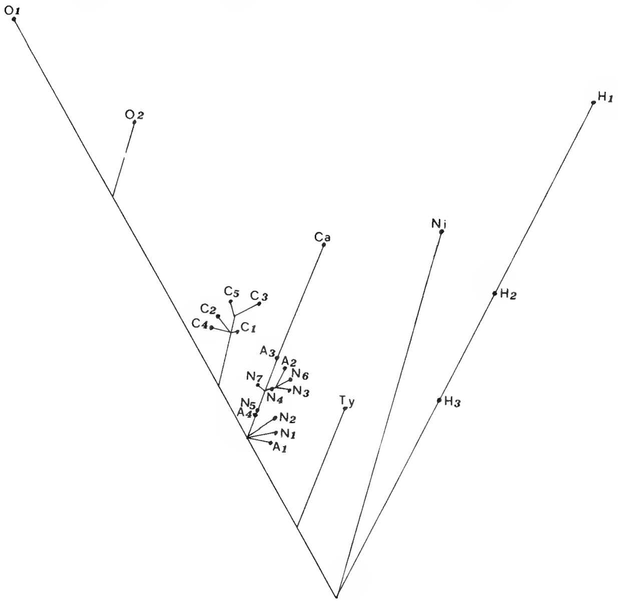

Figure 2. Dendrogram obtained by the Continous Characters Maximum Likelihood method.

5. *E. cassioides* (*E. neleus* + *E. aquitania*), *E. tyndarus* and *E. calcarius* also cluster at similar levels (Nei's **D** [*E. cassioides* - *E. calcarius*] = 0.096 ; [(*E. cassioides* + *E. calcarius*) - *E. tyndarus*] = 0.147).

6. *E. nivalis* is the most genetically distant species of the *E. tyndarus*-*E. cassioides*-*E. calcarius* lineage (Nei's **D** ≈ 0.3).

7. The two populations of *E. ottomana* are genetically rather distant (Nei's **D** = 0.177).

8. Among populations of *E. hispania* the closest are 'ssp. *rondoui*' and 'ssp. *goya*' (Nei's **D** = 0.063), whereas the nominotypical form is genetically quite distinct (Nei's **D** = 0.155).

The UPGMA cluster of Nei's genetic distances is shown in Fig. 1.

The 'phylogenetic' tree obtained by the Continuous Characters Maximum Likelihood Method, is shown in Fig. 2 and concurs with the tree shown in Fig. 1 in all its most important aspects.

Discussion

All our results suggest that the distinction of *E. neleus* and *E. aquitania* is untenable and that this complex is well distinct from *E. nivalis*. The two populations collected at different altitudes on Großglockner, which we identified as *E. cassioides* (low altitude) and *E. nivalis* (high altitude) on characters of wing morphology, show a genetic distance of **D** = 0.358. Accordingly, and apart from other nomenclatural problems (see below) they can be identified as topotypic samples of their respective species.

It remains to be stressed that *E. cassioides* sensu lato is a complex of two genetically different groups of populations. One, including the type locality of *E. cassioides*, occurring at least in the Rhetian Alps and the Tauern. The other includes all populations from the Italian Apennines, the central and western Alps, the Pyrenees and the Cantabrian Mountains. The names by which these groups of populations can be identified will be dealt with further on.

The relatively small genetic distance between these two taxa (Nei's **D** = 0.071) is probably a consequence of them having become separated in recent times. On the basis on Nei's calibration of the molecular clock these two taxa would have started to evolve independently about 0.35 Myr ago. Since this date gene flow was presumably interrupted by the intervening populations of *E. tyndarus*, a species already genetically distinct from the rest, having the fixed allele MPI 70 (absent from all populations of *E. cassioides* s.l. and otherwise only found in *E. hispania*) and lacking the allele PGI 100 (very common in *E. cassioides* s.l.). The interruption of gene flow between eastern and western populations of *E. cassioides* s.l. is demonstrated by the absence of allele 6PGD 100 from populations of the former. Subsequently, the rising temperature may have progressively confined western populations of *E. cassioides* to the mountain peaks of the Alps, Apennines, Pyrenees and Cantabrian Mountains. Nei's distances between these populations generally vary between 0.01 and 0.02, which would place such events in the interval of 50,000 - 100,000 years bp. These distances, however, are too small to be reliable and should be confirmed by independent studies on mitochondrial DNA.

On purely morphological grounds populations of the 'western group' are not easily identified from nominotypical *Erebia cassioides*. The latter generally have slightly smaller size, more rounded wings at apex and are darker grey on ventral surface of the hindwings, with a normally less neatly black edged discal stripe. In females the hindwing colouration is silvery grey on ventral surface, with almost no hint of a yellowish or creamy wash. The opposite applies to populations of the 'western group'.

A potentially interesting field for future research would be to investigate genetic distances between other 'subspecies' having similar distributions, such as those found within *E. pronoe*, *E. meolans*, etc. It may be worth noting that the presence of another species occurring between populations of an eastern and a western group may have contributed to an earlier interruption of the gene flow, as well as to keep the interruption in place by mutual exclusion, when more favourable environmental conditions took over. Where such a situation is lacking, e.g. for *E. euryale*, *E. pluto*, *E. gorge*, etc., there is enough morphological evidence to suggest that hybrid populations exist in between, where they probably represent the outcome of secondary hybridization events.

Another lineage is that of *E. hispania*, where even though no cohabitation can obviously occur between populations of the Pyrenees (N Spain) and Sierra Nevada (S Spain), genetic distances suggest that two different species are involved : *E. hispania* (Sierra Nevada) and *E. rondoui* (Pyrenees). Such a distinction is supported also by their different haploid chromosome complements ($n = 25$ and $n = 24$, respectively) and external morphology.

It is finally worth mentioning that the only two western European populations of *E. ottomana*, the so called 'ssp. *tardenota*' and 'ssp. *benacensis*', sharply differ from each other on a genetic, as well as on a morphological basis. A final word on this subject, however, cannot be spoken until populations from the Balkan peninsula and Turkey have been analyzed.

Nomenclature

1. The application of the name *Papilio cassioides* Reiner & Hohenwarth, 1792.

The reasons why Warren (1981) considered Reiner & Hohenwarths' name a nomen nudum (i.e. a name that fails to conform to Articles 11-13 of the International Code of Zoological Nomenclature, ICZN) have been dealt with already. Such a contention, however, finds little support in the current edition of the ICZN, since the publication of this name not only was accompanied by a description, but a specimen (presumably the holotype), now lost, was also figured. Neither can this name be considered a nomen oblitum (i.e. a forgotten name, a term that has been omitted from recent editions of the ICZN), because it remains by far the most commonly employed name in current literature. On the other hand, however, it is true that although both the description and the accompanying figure are taxonomically obscure, the description may subjectively be presumed to represent the taxon currently referred to as *E. nivalis* Lorković & de Lesse, 1954.

To preserve nomenclatural stability, therefore, we think that the most straightforward nomenclatural option is at this point to select a neotype, in accordance to provisions of Art.75 of the ICZN. Accordingly, we herewith designate the male specimen labeled : Zirknitztal : Großglockner : Austria, 30.07.1991, leg. L. Cassulo, deposited in the collection of the Museo Civico Giacomo Doria (Genoa, Italy) as neotype of *Papilio cassioides* Reiner & Hohenwarth, 1792.

2. Western and southern populations of the *Erebia cassioides* complex.

The discovery that two genetically different groups of populations can be identified within the *E. cassioides* complex resurrects WARREN's (1955, 1981) suggestion, albeit on different grounds, that two different species may have been confused under this name. The name *Erebia neleus* (Freyer, 1833), however, probably cannot be employed for either of these, as it was proposed to designate some electrophoretically still unstudied populations from the Alps of Transsylvania (Retezat Mts) which may prove conspecific with *E. cassioides.*

Should populations of the 'western group' be found to be distinct at species or subspecies level, they should be designated by the name *Erebia* (*cassioides*) *carmenta* (*Erebia tyndarus carmenta* Fruhstorfer, 1909 — Soc. ent., 24 : 223 — type locality : N.Italy : Province of Aosta : Alpi Graie : Courmayeur), rather than *Erebia* (*cassioides*) *aquitania* (*Erebia tyndarus aquitania* Fruhstorfer, 1909 — Soc. ent., 24 : 125 — type locality : Maritime Alps). Although both names bear the same author and date, selecting *carmenta* will have the advantage of avoiding confusion with other treatments of the group. It is rather unfortunate, in this connection, that Reverdin's name '*murina*' cannot be employed, as infrasubspecific, and as such invalid on a nomenclatural basis (*E. tyndarus* var. *cassioides* forma *murina* Reverdin, 1909 — Bull. Soc. lépid. Genève, 1 : 292 — type locality : Le Moléson, Prealps of Freiburg's Gruyère, Switzerland).

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Biochemical taxonomy and evolutionary relationships in *Polyommatus* (subgenus *Agrodiaetus*) (Lepidoptera, Lycaenidae)

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Summary

Relationships between monomorphic species of the subgenus *Agrodiaetus* have been studied by enzyme electrophoresis. Results indicate that all species traditionally recognised on the basis of de Lesse's karyological studies may represent real species. Irrespective of problems of holocentricity it also appears likely that chromosome rearrangements may have contributed to speciation in this group of insects.

Zusammenfassung

Die Beziehungen zwischen den monomorphischen Arten des Subgenus *Agrodiaetus* wurden mit der Hilfe elektrophoretischer Methode untersucht. Die Ergebnisse zeigen, daß die Arten, die gewöhnlich nach de Lesse's karyologischen Untersuchungen anerkannt werden, echte Arten sind. Trotz des Holocentrismusproblems, haben vermutlich "Chromosomen-Rearrangements" in der Artenbildung dieser Insektengruppe eine Rolle gespielt.

Résumé

Les relations phylogénétiques entre les espèces monomorphes apartenant au sous-genre *Agrodiaetus* ont été étudiées au moyen de l'analyse électrophorétique des enzymes. Nos résultats suggèrent que toutes les espèces traditionnellement reconnues dans ce groupe sur la base des études caryologiques conduites par de Lesse, représentent de véritables espèces. Quoi qu'il en soit de l'holocentrisme chromosomique chez les Lépidoptères, il semble aussi très probable que quelque mécanisme de réarrangement chromosomique puisse avoir contribué à la spéciation au sein de ce groupe d'insectes.

Introduction

Members of the subgenus *Agrodiaetus* (Hübner, 1822) are widespread across Europe and Asia, and range from the Iberian peninsula to the Altai Mountains and further to the east, with a distribution characterized by extreme geographical fragmentation.

The identification of species of *Agrodiaetus* can be quite difficult. As a consequence, the systematics of this subgenus goes little beyond alfa-taxonomy and no phylogenetic reconstruction has so far been attempted. Morphological features traditionally employed in butterfly taxonomy, either do not sufficiently differ between species (e.g. male genitalia) or, although variable, are not sufficiently constant at the intraspecific level (e.g. female genitalia, shape of androconial scales, etc.).

So far, therefore, most taxonomic work has been based on characters of wing colouration and markings. In this respect, two groups are traditionally recognized. One includes the so-called dimorphic species, whose males are promptly identified by their blue wings, on the dorsal surface, as opposed to the brown wings of females. The other group includes monomorphic entities only, with dark brown wings in both sexes.

Forster (1956), working on this basis, was the first to attempt a broad revision of *Agrodiaetus*. Since using chromatic characters within the monomorphic forms of the *P. ripartii* complex is impossible, however, his work was almost entirely dedicated to the study of the dimorphic complex.

A major problem deriving from the use of characters such as the shade of the blue colour on the dorsal surface of the male's wings, or the extent and degree of development of submarginal markings on the ventral surface of the hindwings, etc., is that the interpretation of their relative weight may be subjective. Notwithstanding the great importance generally attached to Forster's work, therefore, it is not surprising that solutions offered by this author for some taxonomic problems remain controversial, while others have been abandoned altogether.

The extensive karyological study carried out on members of this and other subgenera of *Polyommatus* by the late Hubert de Lesse while working in the Paris Natural History Museum from the late 1950s (de Lesse, 1957 ; 1959a,b,c,d,e,f ; 1960a,b,c ; 1961a,b ; 1962a,b ; 1963 a,b,c) was immediately welcomed by lycaenid specialists. Characters derived from haploid chromosome complements soon became widely employed in the taxonomy of this group, where they contributed considerable changes. On this basis, many morphologically almost indistinguishable forms of the monomorphic complex have been recognized as distinct species, whereas a number of new species have been described both within this and the dimorphic group.

Not even this study, however, could provide a definitive solution to the biological riddle of *Agrodiaetus*. A first problem is that butterfly chromosomes are normally seen in a contracted state, when they do not show any of the karyological details used to identify homologous regions. What is worse, it soon became apparent that Lepidoptera chromosomes may be holocentric, (see White, 1973 for a review). Should this be true, it is contended, haploid chromosome complements (i.e.'chromosome numbers') would provide little or no evidence for speciation. Holocentric chromosomes, in fact, could conceivably pair with each other almost at any homologous region, and not at the centromeric region only as is usual. For similar reasons they could freely become fragmented, or bind on ends to each other, etc. without necessarily causing any major karyological imbalance. Even though views on this subject seem now to be changing again (see Bigger, 1960 ; Suomalainen, 1969 ; or Lorković, 1990 for a review), haploid complements permit, at least, various interpretations. For example, whereas different haploid complements, as such, perhaps should not be considered sufficient evidence for speciation, when encountered in morphologically similar allopatric populations, the discovery of sharp karyotypic differences between parapatric or sympatric populations may represent a strong argument to assume that gene flow has been interrupted.

For all these reasons, however, the unusually broad variability in haploid chromosome complements currently known to exist within the subgenus *Agrodiaetus* (from n = 7, in *Polyommatus nephohiptamenos* to n = 125, in *P. dolus*), combined with the lack of evidence from crossing experiments to determine levels of hybrid dysgenesis, stimulate questions on whether or not the 60 odd currently recognized species may really all represent biologically distinct taxa.

The purpose of this work is therefore to i) utilize electrophoretically detectable enzyme variability to analyze levels of genetic divergence between karyotypically different sibling species of the monomorphic complex, ii) show relationships among members of this subgenus and finally to iii) suggest a possible evolutionary scenario.

Materials and methods

Preparation of samples

A total of 196 specimens from 21 natural populations of *Agrodiaetus* and 1 population of the subgenus *Lysandra* (*Polyommatus* (*Lysandra*) *corydonius* Herrich-Schäffer, 1852, otherwise known as *P.* (*L.*) *caucasicus* Lederer, 1869), included as outgroup, were collected at several localities in Italy, France, Spain, ex-Yugoslavia and Turkey (Table 1).

Since females are difficult to identify, only adult males were employed. Their wings were immediately removed with sharp scissors and the whole bodies were frozen in liquid nitrogen while still alive. Specimens were stored in this medium for several weeks, until further processing. Samples were prepared for electrophoresis as follows. Individual butterfly bodies were thawed in 250 µl of an ice-cold homogenizing solution (NADP 0.125 mM, 2-mercaptoethanol 1.14 mM ; pH range between 6-8) and macerated with an electric tissue grinder.

Table 1

Populations sampled

Locality	Country, Region	No.	Symbol
Col de Cabre	France, Drôme	13	D1 (*damon*)
Glassier di Ollomont	Italy, Aosta	11	D2 (*damon*)
Tahir	Turkey, Agri	10	D3 (*damon*)
Tragacete	Spain, Cuenca	11	D4 (*damon*)
Les Puits d'Auzon	France, Bouches du Rhône	10	L1 (*dolus dolus*)
L'Hospitalet du Larzac	France, Aveyron	5	L2 (*dolus vittatus*)
Pic du Cougouille	France, Aveyron	10	L3 (*dolus vittatus*)
Ainsa	Spain, Huesca	6	Fu (*fulgens*)
Erzincan	Turkey, Erzurum	9	Me (*menalcas*)
Ainsa	Spain, Huesca	2	R1 (*riparti*)
Akşehir	Turkey, Konya	11	R2 (*riparti*)
Col de Braus	France, Alpes Maritimes	16	R3 (*riparti*)
Koçak	Turkey, Van	10	De (*demavendi*)
Sinkan	Turkey, Ankara	9	A1 (*admetus anatoliensis*)
Küru Dagi	Turkey, Çanakkale	9	A2 (*admetus admetus*)
Nova Breznica	Macedonia	9	A3 (*admetus admetus*)
Gevas	Turkey, Van	10	In (*interjectus*)
Tragacete	Spain, Cuenca	14	Fa (*fabressei*)
Oulx	Italy, Torino	7	Ex (*exuberans*)
Pondel	Italy, Aosta	12	Hu (*humedasae*)
Palandöken	Turkey, Erzurum	10	Ly ((*L.*) *corydonius*)

Centrifugation at 13,000 x g for 15 minutes permitted the separation of a clear supernatant. Care was paid to avoid overheating during both homogenization and centrifugation. Homogenates were stored at –80° C in 5-15 µl aliquots in microtubes.

Electrophoresis

Electrophoresis was carried out on Cellogel sheets at 4° C, as we have found the gel form of cellulose acetate an excellent support medium. An important advantage is that it requires only 0.5-1 µl per sample per enzyme run, whereas other support media require 10-50 µl : this is a remarkable advantage for projects where many enzymes must be scored (often more than once for obtaining best results) from single very small samples.

Buffer systems and staining techniques were similar to those described by MEERA KHAN (1971) and RICHARDSON *et al.* (1986). Genetically interpretable banding patterns could be obtained for : glycerol-3-phosphate dehydrogenase (E.C.1.1.1.8) (αGPD), adenylate kinase (E.C.2.7.4.3) (AK), hexokinase (E.C.2.7.1.1) (HK), glucose-6-phosphate dehydrogenase (E.C.1.1.1.49) (G6PD), malate dehydrogenases (E.C.1.1.1.37) (MDh-1, MDh-2), phosphoglucose isomerase (E.C.5.3.1.9) (PGI), glutamate-oxaloacetate transferases (E.C.2.6.1.1) (GOT-1, GOT-2), malic enzyme (E.C.1.1.1,40) (ME), 6-phosphogluconate dehydrogenase (E.C.1.1.1.44) (6PGD), phosphoglucomutase (E.C.2.7.5.1)

(PGM), esterases (E.C.3.1.1.1) (ES-1, ES-2). Isozymes and alleles were designed numerically according to their decreasing mobility rate.

Statistical analyses

Average probabilities of interpopulation genetic distance were estimated by Nei's (1972) I and D related indexes (jackknifed according to Mueller & Ayala, 1982), on the basis of fourteen shared loci and for pairwise combinations of all populations investigated.

Results and discussion

The cumulative total of alleles detected at the fourteen shared loci is 67 (range 3-9). Allele frequencies are reported in table 2. Nei's genetic index **D** was employed to generate the cluster shown in Fig. 1. While the distance between the subgenera *Agrodiaetus* and *Lysandra* shows, as expected, a relatively high level of genetic differentiation (**D** = 0.625), the split sequence and branch lengths within the subgenus *Agrodiaetus* are rather unexpected. A second split separates *P. damon* samples (**D** = 0.460) from all the rest. The separation between monomorphic and dimorphic forms occurs at **D** = 0.20.

From the dendrogram the following phylogenetic reconstruction can be inferred :

1. *Polyommatus* (*Lysandra*) *corydonius* lies on a different lineage with respect to all the populations of *Agrodiaetus*. The latter, accordingly, may be considered a monophyletic group (subgenus).

2. Within the phyletic line of *Agrodiaetus*, the four studied populations of *P. damon* group on a distinct branch.

3. Another branch includes all monomorphic populations, together with *P. dolus*, *P. dolus vittatus*, *P. fulgens* and *P. menalcas*. Males of both monomorphic and dimorphic forms in this phyletic line are provided with androconial scale-tufts ('sex-brands'). The close relationships within the latter lineage support an old, non phylogenetically-based suggestion by de Lesse (1960a), who divided *Agrodiaetus* into two main groups : the *P. ripartii* complex, including both monomorphic and dimorphic forms with androconial scale-tufts in males, and the *P. damon* group, where sex-brands are absent.

Distances between members of both complexes are indeed very small, but not incompatible with those encountered between sibling species of other groups (Mensi *et al.*, 1988 ; 1992). The central point, in this respect, is represented by the pivotal position assumed in the dendrogram by *P. admetus*. This is, in fact, about the only easily identifiable species within the monomorphic complex. *P. admetus* is widely distributed from "Yugoslavia" to East Turkey and, apart from flying with many other species of the dimorphic group (*P. menalcas*, *P. hopfferi*, etc.), is often encountered in cohabitation with e.g. *P. ripartii* (Greece, Turkey, etc.), *P. demavendi* or *P. interjectus* (Turkey). Since its species-level separation from all other species of the monomorphic complex

Table 2

Allele Frequencies at 14 shared non-monomorphic loci in 21 populations. Populations are numbered as in Table 1. For some enzyme not all individuals of all populations were scored. '-' indicates that in the population scoring was not possible. In some cases numeration of alleles takes into account populations not included in this work.

		D1	D2	D3	D4	L1	L2	L3	Fu	Me	R1	R2	R3	De	A1	A2	A3	In	Fa	Ex	Hu	Ly
αGPD	1		0.05	0.05																		
	2	1.00	0.95	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	3													0.05								
AK	1	0.72	0.61	0.50	1.00																	
	2	0.28	0.39	0.50		1.00	1.00	1.00	1.00	1.00	0.75	1.00	0.94	1.00	1.00	1.00	1.00	1.00	1.00		1.00	0.80
	3										0.25		0.06							1.00		0.20
HK	1																					1.00
	2	1.00	1.00	0.80	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	1.00	1.00	1.00	
	3			0.20														0.06				
G6PD	1																					
	2				0.12																	
	3	1.00	1.00	1.00	0.87																	
	4														0.22					0.14		
	5					1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.78	1.00	0.94	1.00	1.00	0.86	1.00	
	6																					
	7																0.06					1.00
	8																					
	9																					
MDH-1	1								0.08					0.06			0.56					
	2	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.92	1.00	1.00	0.95	1.00	0.69	0.78	0.50	0.44	0.75		1.00	0.96	0.85
	3											0.05		0.25	0.22	0.50		0.25	1.00		0.04	0.15
MDH-2	1												0.21									
	2	0.15	0.41		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.79	1.00	0.87	1.00	1.00	1.00	0.89	0.50	1.00	1.00
	3	0.85	0.59	1.00											0.12				0.11	0.50		
PGI	1											0.05										
	2	0.04						0.11	0.08			0.09		0.05			0.06	0.05		0.21		
	3																					
	4	0.92	1.00	1.00	1.00	0.85	0.50	0.50	0.75	0.94	1.00	0.73	0.62	0.70	0.78	0.83	0.89	0.90	0.46	0.79	1.00	0.85
	5							0.06				0.14	0.35	0.10								
	6	0.04				0.15	0.50	0.33	0.17	0.06			0.04	0.05	0.22	0.17	0.06	0.05	0.54			0.15
	7													0.10								

		D1	D2	D3	D4	L1	L2	L3	Fu	Me	R1	R2	R3	De	A1	A2	A3	In	Fa	Ex	Hu	Ly
GOT-1	1		0.25																			
	2	1.00	0.75	0.65	0.14									0.20			0.06	0.61				0.15
	3					1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.55	1.00	1.00	0.94	0.39	1.00	1.00	1.00	
	4																					0.85
	5																					
	6			0.35	0.86									0.25								
GOT-2	1	0.17	0.25		0.25										0.06	0.11						
	2	0.83	0.62	1.00	0.75	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	0.89	1.00	1.00	1.00	1.00	1.00	
	3		0.12																			1.00
	4																					
ME																						
	1		0.17		0.09																	
	2	1.00	0.83	1.00	0.91	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.55
	3																					0.45
6PGD	1							-				-	-	0.15	0.06	0.06						
	2					1.00	1.00	-	1.00	0.81		-	-									
	3							-			1.00	-	-	0.20	0.17	0.22	0.19		1.00	1.00		
	4	0.92	1.00	1.00	0.75			-		0.19		-	-	0.65	0.78	0.72	0.81	1.00			1.00	1.00
	5	0.08			0.25			-				-	-									
PGM	1	0.14		0.25																		0.25
	2	0.86	1.00	0.75	1.00	0.10			0.08	0.56				0.50							1.00	0.65
	3									0.33	1.00	1.00	1.00	0.33	1.00	1.00	1.00	1.00	1.00	1.00		
	4																					
	5					0.40	1.00	1.00	0.92	0.11				0.17								0.10
	6					0.50																
EST-1	1	-						-				-	-									0.75
	2	-						-				-	-									
	3	-	1.00	1.00	1.00	1.00	1.00	-	1.00	0.83	1.00	-	-	0.85	1.00	1.00	1.00	0.89	0.93	0.93	1.00	0.25
	4	-						-		0.17		-	-									
	5	-						-				-	-	0.15				0.11	0.07	0.07		
EST-2	1							-				-	-									0.10
	2					0.05	0.60	-	0.33			-	-	0.15					0.75			0.90
	3							-				-	-								1.00	
	4					0.95	0.40	-	0.67	1.00	1.00	-	-	0.85	1.00	1.00	1.00	0.95	0.25	0.75		
	5	1.00	0.86	1.00	0.95			-				-	-							0.25		
	6							-				-	-									
	7		0.14		0.06			-				-	-					0.05				

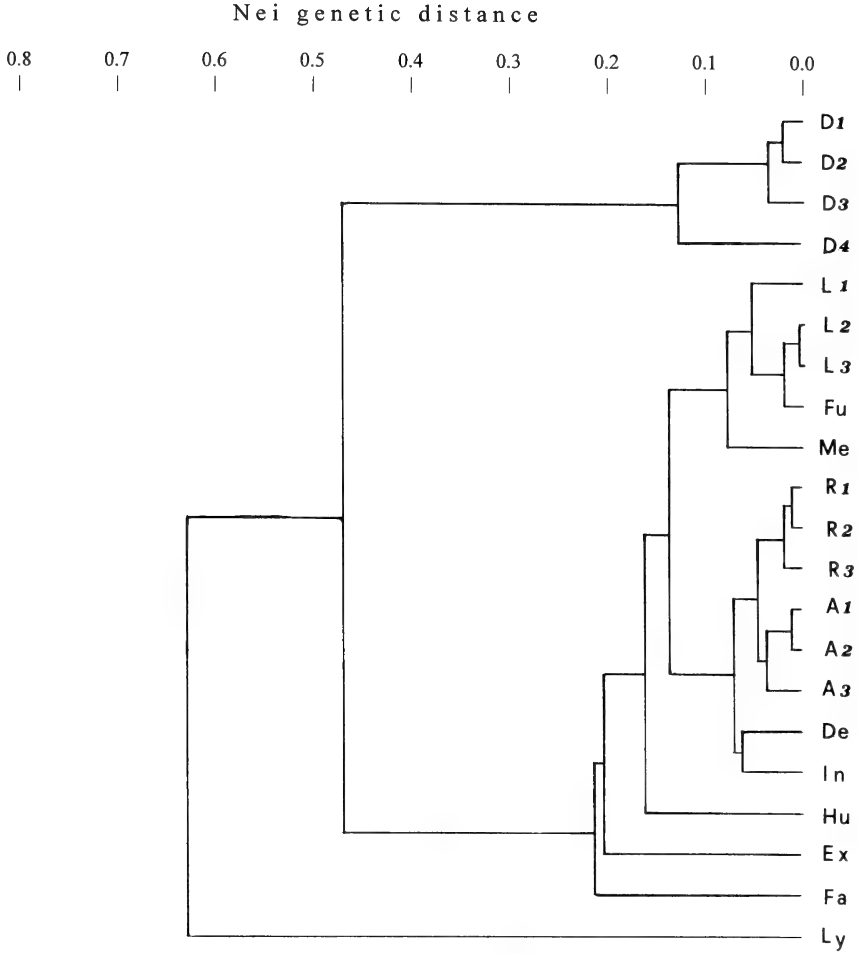

Figure 1. Dendrogram based on Nei's Distances. All nodes shown are statistically different from zero.

is unquestionable, its level of genetic divergence with respect to *P. ripartii*, on the one hand, and *P. demavendi* and *P. interjectus*, on the other, can be taken as a yardstick to infer that all other chromosomically- identified 'species' within the monomorphic complex may indeed qualify as biologically distinct sibling species. Conversely, even though a more detailed analysis is required, also extending to the dimorphic species group, our results are not incompatible with the hypothesis that, in the case of *Agrodiaetus*, karyological mechanisms may have been involved in speciation processes.

Based on Nei's rough estimates for the (highly controversial) molecular clock hypothesis, it may be possible to approximately date the branching events as follows : the subgenus *Agrodiaetus* originated about 3.1 Myr ago (i.e. in the late Pliocene) as dimorphic, sex brand-lacking forms (plesiomorphic characters) ; monomorphism and scale-tufts appeared later, roughly 2.3 Myr ago. Finally, the ancestors of the *Agrodiaetus dolus* group diverged only about 1 Myr ago. The dimorphic character of this complex is therefore of a secondary origin, and may be derived from a simple reverse mutation which took place within the monomorphic complex. Speciation events within the monomorphic complex are indeed very recent, generally in the 50,000-100,000 years bp interval. These distances, however, are too small to be reliable and should be confirmed by independent studies on mitochondrial DNA. The most important exceptions, in this respect, are represented by *P. fabressei* , *P. exuberans* and *P. humedasae*, which, in this order, are the most primitive taxa of the monomorphic group. It may be interesting to note that, apart from *P. admetus*, *P. fabressei* is the only other monomorphic species commonly encountered in cohabitation with another species of this same complex (with *P. ripartii* in the Montes Universales region : central Spain cf. DE LESSE, 1961c and personal observations).

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A preliminary review of the classification of the zygaenid subfamily Procridinae (Lepidoptera)

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Summary

In his revision of the Zygaenidae of the world, Alberti (1954) divides the Zygaenid subfamily Procridinae into the two tribes Callizygaenini and Procridini. As typical for the subfamily, he mentions 9 main characters ("Leitmerkmale"). Three of them refer to the head and the wing, the other six to the sclerotized parts of the genitalia of the male and female. Studies of type material from all regions of the world have shown that the real autapomorhies of the Procridinae are found in the interior female genitalic structures. Of the nine characters mentioned as typical for Procridinae by Alberti, none is unique to this subfamily as all of them are shared with at least one other group of Zygaenidae. Therefore they cannot be used as autapomorphies for the Procridinae. As the type species of the tribe Callizygaenini, *Callizygaena auratus* (Cramer, 1779) (= *nivimacula* Felder, 1874), lacks the autapomorphies of the subfamily Procridinae, the tribe has to be excluded from the Procridinae and is considered to form a distinct subfamily of the family Zygaenidae. The remaining species in the Procridinae can be divided into two groups, the *Adscita-Illiberis*-group and the *Artona*-group. Both are considered to form well-separated tribes within the subfamily. The *Adscita-Illiberis*-group has a world-wide distribution, whereas the *Artona*-group is restricted to the Indo-Australian and Afrotropical regions with a few species occurring also in the eastern Palaearctic region. Observations on the biology support the evidence provided by results based on morphological characters.

The monophyly of the Procridinae

The Procridinae are the only subfamily of the Zygaenidae with a world-wide distribution, whereas all other subfamilies are restricted to smaller areas. On the American and Australian continents they are the only representatives of the family. The nine principal characters ("Leitmerkmale" sensu Alberti) of the Procridinae are :

1. Proboscis only sometimes reduced
2. Chaetosemata always present

3. Analis [CuP] always present
4. Ovipositor absent
5. Ductus seminalis inserted into corpus bursae near orifice of ductus bursae (and not from ductus bursae itself)
6. Ductus bursae frequently with specialized structures
7. Uncus single and pointed, without sensory hairs
8. Valva well developed
9. Aedeagus never thorn-shaped

A critical review of these characters shows that not one of them is a real autapomorphy of the subfamily, as the Procridinae share most of them with at least one other subfamily of the Zygaenidae.

Notes

ad 1) As far as is known the proboscis is reduced in only two genera of Procridinae (*Theresimima* Strand, 1917 [1 species] and *Rhagades* Wallengren, 1863 [1 of 4 species]) in which it is approximately two-thirds shorter than normal. It is fully developed in all Zygaeninae except in the relict species *Pryeria sinica* Moore, 1877, and in nearly all the Chalcosiinae except a few genera in which it is shorter (e.g. *Aglaope* Latreille, 1809, *Chalcosiopsis* Swinhoe, 1894, *Boradia* Moore, 1879). It is partly reduced in the Phaudinae and totally absent in the Anomoeotinae and Himantopterinae. These three groups are treated as subfamilies of the Zygaenidae by ALBERTI (1954). The Anomoeotinae and Himantopterinae are now accepted as distinct families within the superfamily Zygaenoidea and the Phaudinae may also form a separate family perhaps including the *Lactura*-group according to larval and female genitalic characters (Kirky, pers. comm.). Within the remaining three subfamilies of Zygaenidae, the Zygaeninae, Chalcosiinae and Procridinae, the character 'proboscis only sometimes reduced' does not represent an autapomorphy of the Procridinae.

ad 2) Well developed chaetosemata are present in all Zygaeninae, Chalcosiinae and Procridinae. The presence of chaetosemata is therefore a family character of the Zygaenidae.

ad 3) The vein CuP (analis sensu ALBERTI, 1954) is present in all Zygaeninae, Chalcosiinae and Procridinae. It is therefore a family character of the Zygaenidae.

ad 4) Absence of an ovipositor occurs in all Zygaeninae and in all Procridinae, except the Central American genus *Gonioprocris* Jordan, 1913 in which a small ovipositor is developed. A well developed ovipositor is present in the Chalcosiinae. As this character is shared by both the Zygaeninae and Procridinae it cannot be an autapomorphy of the subfamily Procridinae and is considered to be plesiomorphic.

ad 5) The ductus seminalis is inserted into the ductus bursae near the antrum in the Zygaeninae and in some Chalcosiinae (e.g. tribe Heteropanini), but arises from the corpus bursae in most Chalcosiinae and all Procridinae. Therefore this character does not represent an autapomorphy of the subfamily Procridinae.

ad 6) The ductus bursae has many very strange and specialized structures in most Procridinae but there are also groups within this subfamily in which the ductus is simple. The specialization of the ductus bursae (e.g. the evolution of a praebursa) is a good autapomorphy for certain subgroups of the Procridinae but not an autapomorphic character for the entire subfamily.

ad 7) It is true that nearly all Procridinae have a single and pointed uncus mainly without any sensory hairs. All Zygaeninae and many Chalcosiinae (e.g Chalcosiini) have a double uncus. In those Chalcosiinae in which a single uncus is developed (e.g. Cyclosiini), it is rarely pointed and bears sensory hairs. Nevertheless there are some Chalcosiinae which have a single uncus which lacks hair (e.g some *Cyclosia* Hübner, [1820]) and there are specializations of the uncus known in some Procridinae (e.g. *Neoprocris* Jordan, 1915). Therefore this character is also not a good autapomorphy of the subfamily Procridinae.

ad 8) All Zygaeninae, Chalcosiinae and Procridinae have a well-developed valva which is a plesiomorphic character.

ad 9) The aedeagus is thorn-shaped in the tribes Agalopini, Aglaopini and Chalcosiini of the subfamiliy Chalcosiinae, but normal and tube-like in the tribes Cyclosiini and Heteropanini. In all Zygaeninae and Procridinae it is not thorn-shaped. The character 'aedeagus never thorn-shaped' does not represent an autapomorphy of the subfamily Procridinae.

Although according to recent research the characters of Alberti do not represent good autapomorphies of the subfamily there is no doubt that this group is a monophyletic unit and its status as a subfamily of the Zygaenidae is justified. The main characters that clearly separate the Procridinae from all other Zygaenid subfamilies are :

1. *Female genitalia with ductus seminalis lacking pseudobursa or bulla seminalis.*

As in most families included in the superfamily Zygaenoidea, there is a well-developed pseudobursa present in the Zygaeninae and Chalcosiinae. The lack of a pseudobursa in the Procridinae is therefore considered to be a secondary reduction, or plesiomorphic.

2. *Lagena in receptaculum seminis absent.*

In Zygaeninae and Chalcosiinae and, as far as checked, in all other families included in the superfamily Zygaenoidea a well-developed lagena is present, as in most ditrysian Lepidoptera. The reduction of the lagena in the Procridinae is therefore considered to represent a good autapomorphic character of the group.

3. *A pair of accessory glands is present close to the ooporus which may represent a structure homologous to Petersen's gland in the Zygaeninae.*

These glands differ in shape and structure from those of the Zygaeninae. They are lacking in the Chalcosiinae. There is one group of Procridinae in which these glands are secondarily reduced or transformed into a different structure (*Pollanisus* Walker, 1854, *Hestiochora* Meyrick, 1887 and *Onceropyga* Turner, 1906 in Australia). According to recent research Petersen's gland in the Zygaeninae produces a secretion which is supposed to prevent predators and possibly funghi from attacking the eggs (Naumann, pers. comm.). As the Australian group is not able to produce this liquid due to the absence or the modification of the glands another defence system has been developed. The females of the three above-mentioned Australian genera are characteristized by their abdominal hairtuft. When laying eggs the long, hair-like scales of this hairtuft are glued to the surface of the eggs, giving the egg clusters a hedgehog-like appearance. The tips of these scales are poisonous and an aphid, for example will die within a quarter of an hour after touching them. It is therefore possible that the glands have evolved into a special subcuticular poisonous area in which the spiny scales are situated. When the scales become attached to the egg by their distal part, the proximal part is covered with poison as in a poisonous dart.

4. *Larva without chemical defence system.*

In the larvae of Zygaeninae and Chalcosiinae a special cuticular defence system is present (POVOLNÝ & WEYDA, 1981 ; FRANZL & NAUMANN, 1984 ; 1985 ; WITTHOHN & NAUMANN, 1984a ; 1984b). Similar defence systems have also been discovered in other Zygaenoidea (Naumann, pers.comm.). It is not yet clear whether the lack of such a cuticular defence system in larvae of the Procridinae is a secondary loss or a primary situation.

The subdivision of the Procridinae into tribes

ALBERTI (1954 : 209), in his revision of the family, divided the subfamily Procridinae into the two tribes Callizygaenini and Procridini. He was convinced that both are monophyletic units within a monophyletic subfamily. His opinion was based on studies especially of genitalia structures and the presence or absence of a medial stem in the wing venation. Unfortunately Alberti did not check *Callizygaena aurata* (Cramer, 1779)(= *nivimacula* Felder, 1874), the type-species of *Callizygaena* Felder, 1874. This species and a small group of other congeneric South East Asian species lack the characteristic autapomorphies of the subfamily Procridinae.

The following characters show that the *Callizygaena*-group neither belong to the Procridinae nor to the Zygaeninae or Chalcosiinae :

1. Valva dish-like and strongly sclerotized as in Zygaeninae, with setae at distal margin pointing inwards but with one single, stout, triangular, not

distally pointed and very strongly sclerotized uncus (in the Zygaeninae there is a double-lobed uncus present and in the Procridinae and Chalcosiinae the valva is completely different, never so strongly sclerotized and distally rounded) (Fig. 1).

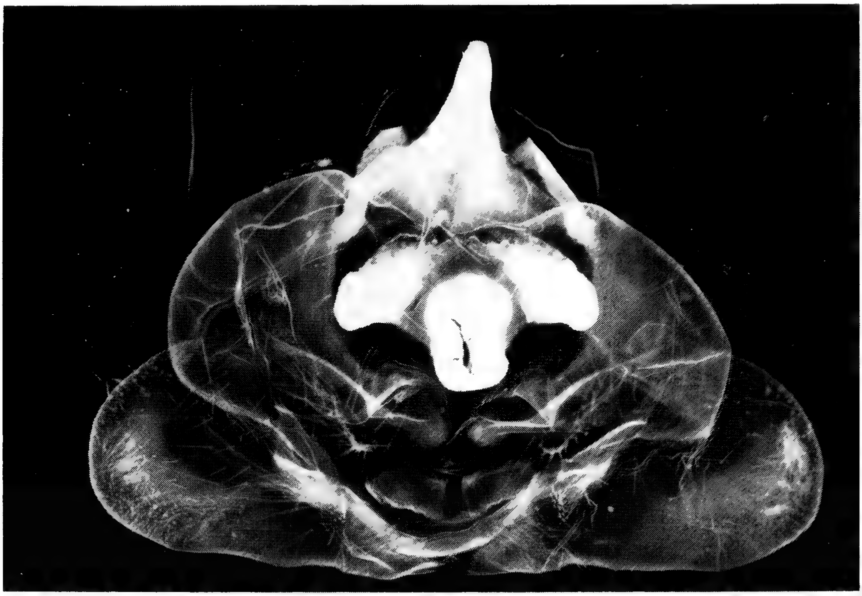

Fig. 1. Male genitalia (Valva-tegumen-uncus-part) of *Callizygaena aurata* (Cramer, 1779), S. India, Mullacore (BMNH/London).

2. Aedeagus a tiny, slender and straight spine (in Procridinae tube-like and much larger compared with the size of the specimens and in the Zygaeninae also much larger with a lamina dorsalis and lamina ventralis present).
3. Corpus bursae with characteristic signa (signa never present in the Procridinae).
4. Ductus seminalis arising from the proximal part of the ductus bursa and not from the corpus bursae (as in the Procridinae) or from the distal part of the ductus bursae (as in the Zygaeninae).
5. A pseudobursa (= bulla seminalis sensu Alberti) is present, as in the Zygaeninae and Chalcosiinae (absent in the Procridinae).
6. Receptaculum seminis with well developed lagena, as in all Zygaenoidea except the Procridinae.

7. Petersen's gland or homologous structures absent (present in the Zygaeninae and Procridinae, also absent in the Chalcosiinae).

Consequently, the *Callizygaena*-group of the Zygaenidae has to be excluded from the subfamily Procridinae and treated as a distinct subfamily of the Zygaenidae, **Callizygaeninae stat.n.**

According to the author's studies the remaining genera of Procridinae can be placed into two subgroups or tribes :

(a) Tribus Procridini Boisduval, [1828]

(b) Tribus **Artonini trib. n.**

The tribe Procridini is still a mixture of several monophyletic subgroups which may be described as separate tribes later, if necessary. The tribe Artonini is a monophyletic unit based on the following autapomorphies :

1. Chaetosema triangular, extending forward between the compound eye and the ocellus (Fig. 2). In all other Procridinae the space between the compound eye and the ocellus is covered with smooth, flat scales and the chaetosema is not extended.

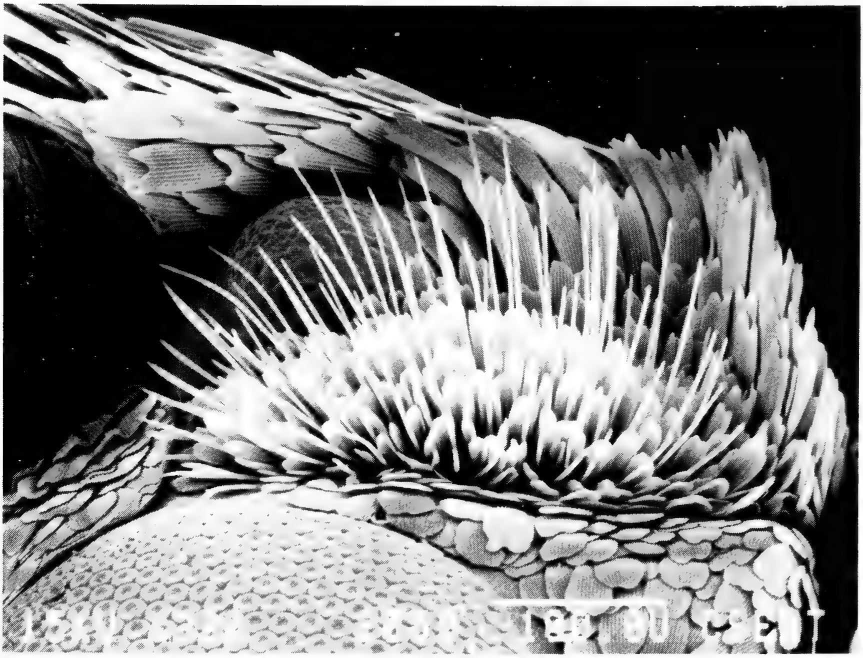

Fig. 2. Chaetosema of a primitive Artonini from Australia. SEM-photo by Colin Beaton, CSIRO, Canberra, Australia.

Fig. 3. Lateral view of a female *Turneriptocris coronias* (Meyrick, 1886) with dorsolateral evagination at abdominal segment 2 (see arrow). Photo by John Green, CSIRO, Canberra, Australia.

2. Abdomen with small dorsolateral evaginations on segments 2 and 7 (Fig. 3). These evaginations are secondarily reduced in some subgroups. Only on the second abdominal segment are these lateral evaginations present in the Australian genus *Pollanisus* Walker, 1854, and there are no lateral evaginations in the Australian genus *Hestiochora* Meyrick, 1887, but as *Hestiochora* is closely related to *Pollanisus* and there are clear synapomorphies indicating the monophyly of these two genera, the reduction of the lateral evagination has to be interpreted as a secondary loss.
3. Valva fan-shaped with a stronger, sclerotized costal and basal margin and a very translucent, strongly folded central part. This type of artonoid valva is present in its basic and simple form in the primitive Australian genera (e.g. *Pollanisus* Walker, Fig. 4) while it has evolved into very complicated structures in most of the tropical genera. However, even if the structures are very complicated the ground-plan of the fan-shaped artonoid valva is still visible.

The Procridini have a world-wide distribution with the exception of the temperate parts of Australia. The Artonini occur only in the Afrotropical Region, in South East and East Asia and Australia, including the temperate parts and the island of Tasmania.

Conclusion

Having excluded the former tribe Callizygaenini from the subfamily Procridinae, the remaining genera within the latter form a monophyletic unit. The

Fig. 4. Artonoid valva type of a primitive Artonini, *Pollanisus subdolosa* (Walker, 1865), male Holotype, Australia (BMNH/London).

monophyletic origin of the Procridinae is supported by four autapomorphies. The subfamily is newly divided into two tribes. The tribe Procridini consists of several monophyletic groups and subgroups, but at the present time there are no characters known which are clear autapomorphies of the whole tribe. The tribe Artonini is monophyletic, based on three autapomorphies. The Callizygaeninae are considered to form a distinct subfamily of the Zygaenidae.

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List of other presentations and posters

AGASSIZ, D. & NASH, P. : The invasion of Britain by *Phyllonorycter leucographella* and other Lepidoptera.
BUSZKO, J. : Marshlands and distribution limits of some Lepidoptera in eastern Poland.
BYUN, B. K. & PARK, K.-T. : Systematic importance of the 8th abdominal segment of male Tortricinae (Tortricidae). [Poster]
COOK, M. A., HARWOOD, L.M., SCOBLE, M. J. & MCGAVIN, G. C. : Geoverdin : A novel pigment from the wings of moths (Geometridae) and the development of a fingerprinting technique for pigments.
DANTART, J. : Notes on the genus *Chesias* (Lepidoptera, Geometridae). [Poster]
DE JONG, R. : Habitat preference, speciation and biogeography.
DE OLANO, I. & MENDEZ, J. M. : Geometridae del Pais Vasco. [Poster]
DIEHL, E.-W. : Can the tropical rain-forests be saved?
EFETOV, K. A. : On the biology and taxonomy of the genus *Adscita* Retzius, 1783 (Zygaenidae). [Poster]
FIEDLER, K. : Vibratory signals of lycaenid caterpillars.
HÄUSER, C. L. : Critical comments on the phylogenetic relationships within the family Papilionidae.
IVINSKIS, P. : Some characteristics of the Lithuanian Lepidoptera. [Poster]
KLJUCHKO, Z. : Die Noctuidenfauna des Daurischen Naturschutzgebietes. [Poster]
KONONENKO, V. S. & MIKKOLA, K. : Taxonomy and zoogeography of the Palaearctic autumn and spring fauna of Noctuidae.
KOZLOV, M. V. : On the origin and phylogeny of the Papilionida (= Lepidoptera).
KOZLOV, M. V. : Population structure and morphological variations of *Micropterix maschukella* Alph. (Micropterigidae). [Poster]
KRISTENSEN, N. P. : Structural diversity in the lowest moths : Some startling new discoveries.
LAFONTAINE, J. D. : Classification of Lepidoptera : Stability through cooperation. [Inaugural lecture]
LAFONTAINE, J. D. : Classification of trifid noctuids : adult and larval conflicts.
LHONORÉ, J. & FAILLIE, L. : L'Azure des Mouillères (*Maculinea alcon* D. & S.), un exemple d'étude de la dynamique de populations dispersées.
MASÓ, A. : Morphology of the Iberian Lepidoptera. [Poster]
MEY, W. : Intraspezifische Konkurrenz bei *Leucoptera malifoliella* (Lyonetiidae) durch induzierte Resistenz am Apfel.
MEYER, M. : Endemic Lepidoptera from Madeira and Azores. [Poster]
MEYER, M. : The variability of endemic macrolepidoptera from the northern part of Macaronesia. [Poster]

Munguira, M. L., Martin, J., Thomas, J. A. & Elmes, G. W. : Host specificity and population dynamics in the Iberian *Maculinea* species (Lycaenidae).

Naumann, C. : Reproductive biology in the zygaenid moths.

Nikusch, I. : New results concerning the subspecies of *Parnassius apollo* and *P. mnemosyne* in Fennoscandia.

Olivella, E. & Sarto i Monteys, V. : Incidence of *Phyllonorycter corylifoliella* (Gracillariidae) on apple orchards in areas of Lleida (Catalonia, Spain). [Poster]

Park, K.-T. : Systematic revision of the tribe Teleiodini in Korea (Gelechiidae). [Poster]

Rákosy, L. : Endangered Macrolepidoptera in Romania. [Poster]

Rákosy, L. : Noctuidae from Romania : Systematic list providing ecological and zoogeographical data. [Poster]

Ronkay, G. & Ronkay, L. : On the phylogeny of the noctuid subfamily Cuculliinae : a provisional sketch of the new system.

Sarto i Monteys, V. & Masó, A. : Remarks on the biology of a lycaenid butterfly, pest of geraniums, new to Europe.

Scoble, M. J. : The family Hedylidae : A revised concept of the butterflies.

Settele, J., Frey, W., Bink, K. & Pfeifer, M. A. : Verbreitung, Ökologie und Schutz vermeintlich gefährdeten Bläulinge in Feuchtwiesen des Oberrheinsgrabens : *Lycaena dispar*, *Maculinea teleius* und *M. nausithous* in the Palatinate.

Sinev, S. Yu. : Some results of the Russian-Finnish expeditions to Siberia and central Asia : Momphidae and some other microlepidoptera. [Poster]

Skalski, A. V. : The possibility of influence of phenological factors on composition of the Lepidoptera in the Baltic and Saxonian amber.

Šulcs, I. : Arten mit östlichen und südöstlichen Verbreitung in Lettland.

Tshistjakov, Y. A. : The current state of the rare and endangered species of the Lepidoptera in the Russian Far East and their conservation.

Väisänen, R. & Laitala, L. : On the ecology of *Lopinga achine* (Satyridae). [Poster]

van Oorschot, H. & van den Brink, H. : Biological and taxonomical aspects of *Melitaea persea* (Kollar, 1849) (Nymphalidae).

Varga, Z. S. : Biogeographic patterns of speciation in some xeromontane Noctuidae genera. [Poster]

Varga, Z. S. : Life history of some butterfly species in the nature reserves in NE-Hungary.

Viidalepp, J. : Cladistic analysis of the genera of Larentiinae (Geometridae) of the temperate to northern Palaearctic.

Weintraub, J. D. : The higher classification of the Lithinini (Geometridae).

Woiwod, I. P. : Mobility and variability in the farmland moth community. [Poster]

Yela, J. L. & Herrera, C. M. : The seasonal cycle of noctuid moths (Noctuidae) and woody plants in Mediterranean montane forests. [Poster]

Ylla i Ullastre, J. : Warm up and flight body temperature of *Graellsia isabelae* (Saturniidae).

In addition to these presentations, short communications were presented at three workshops : Noctuidae, Microlepidoptera and Larvae.

List of delegates

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